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TEXT-BOOK OF PALAEONTOLOGY

TEXT-BOOK

OF

PALAEONTOLOGY

BY

KARL A. VON ZITTEL

PROFESSOR OF GEOLOGY AND PALAEONTOLOGY IN THE UNIVERSITY OF MUNICH

TRANSLATED AND EDITED BY

CHARLES R. EASTMAN, Ph.D.

ASSISTANT IN PALAEONTOLOGY IN THE MUSEUM OF COMPARATIVE ZOOLOGY
AT HARVARD COLLEGE, CAMBRIDGE, MASS.

ENGLISH EDITION REVISED AND ENLARGED BY THE AUTHOR AND EDITOR
IN COLLABORATION WITH THE FOLLOWING SPECIALISTS:

C. E. BEECHER, J. M. CLARKE, W. H. DALL, G. J. HINDE, A. HYATT, J. S. KINGSLEY, H. A. PILSBRY
C. SCHUCHERT, S. H. SCUDDER, W. P. SLADEN, E. O. ULRICH, C. WACHSMUTH

VOL. I. WITH 1476 WOODCUTS

London

MACMILLAN AND CO., LTD.

NEW YORK: MACMILLAN & CO.

1900

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EDITOR'S PREFACE

THE *Grundzüge der Palaeontologie*, which forms the basis of the present work, was published in the spring of 1895, only a short time after the completion of the fifth and last volume of Professor von Zittel's celebrated *Handbuch der Palaeontologie*. Of the latter, an excellent translation exists in French by Barrois; but English-speaking students are without either an independent treatise on Palaeontology or translation from any foreign work, which is comparable in scope and character to the writings of von Zittel.

With the hope of supplying this deficiency the Editor undertook the task of rendering the *Grundzüge* into English. It was at first intended to bring out a strictly literal translation, but with the Author's consent this plan was modified in important respects which should be clearly understood by all. The chapters on *Protozoa* and *Coelenterata* stand here essentially as in the original, but nearly all the remaining chapters have been remodelled, enlarged, and brought as nearly as possible up to date by a selected body of experts.

The greater part of the work is therefore a composite production, and from the nature of the case some incongruities in style and treatment are to be expected. For all the collaborators to have adhered to uniform limits of alteration and expansion would have been impossible. It will be found, therefore, that some portions of the revised text are not sensibly different from the original while others are changed very radically, and a few chapters, notably the *Molluscoidea*, *Mollusca*, and Trilobites, are entirely rewritten. An effort has been made throughout to adapt the text more especially to the needs of Anglo-American students, and the bibliographies have been enlarged with similar intent.

For all changes in the classification over the original the revisers of the different sections are responsible; but although radical departures have been made with the Author's sanction, one must by no means presume he is thereby committed to all the innovations which are set forth. How far and whether in all cases the system has been improved must be left for experience to determine. The Author's graciousness, however, in yielding his own preferences on systematic points will be apparent on reading the subjoined preface.

Due acknowledgments are rendered the collaborators in the Author's

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preface, and also in footnotes at the end of the several chapters. Their names are enumerated below in the order of their respective sections, and the Editor begs to express at this time a sense of his profound appreciation of the services that have been so generously rendered. For the many personal courtesies extended, he would return to each of them his sincere and hearty thanks.

LIST OF COLLABORATORS

Mr. Charles Wachsmuth, *Crinoidea*, *Blastoidea*.
Mr. W. Percy Sladen, *Asterozoa*, *Echinozoa*.
Dr. George Jennings Hinde, *Vermes*.
Mr. Edward O. Ulrich, *Bryozoa*, *Ostracoda*.
Mr. Charles Schuchert, *Brachiopoda*.
Dr. William H. Dall, *Pelecypoda*.
Prof. Henry A. Pilsbry, *Gastropoda*.
Prof. Alpheus Hyatt, *Cephalopoda*.
Prof. Charles E. Beecher, *Trilobita*.
Prof. John M. Clarke, *Eucrustacea (pars)*, *Acerata (pars)*.
Prof. John S. Kingsley, *Eucrustacea (pars)*, *Acerata (pars)*.
Prof. Samuel H. Scudder, *Insecta*.

The Editor is also greatly indebted to his friend Dr. John C. Merriam, who undertook the translation of the entire chapter on *Mollusca*, a very laborious work. Dr. Merriam's assistance has been further enlisted in the translation of the second volume, which will be devoted exclusively to the Vertebrates. Dr. August F. Foerste was kind enough to furnish a translation of the chapter on Insects, and various friends have assisted in correcting proofs. For the compilation of the index the Editor is indebted to Miss Elizabeth B. Bryant, a former student of his at Radcliffe College, and to his brother, Mr. David P. Eastman.

CHARLES R. EASTMAN.

Harvard University,
September 15, 1899.

AUTHOR'S PREFACE

Die englische Ausgabe meiner Grundzüge der Palaeontologie hat ein vom deutschen Original in verschiedener Hinsicht abweichende Gestalt erhalten. Der Herausgeber, mein Freund und ehemaliger Schüler Dr. Eastman, suchte mit meiner Zustimmung eine Anzahl der hervorragendsten Specialisten für die Bearbeitung einzelner Thierclassen zu gewinnen. Dadurch erfuhr das Werk eine gründliche und sachkundige Ueberarbeitung, welche sich namentlich im Detail vortheilhaft geltend macht und mancherlei Irrthümer der deutschen Ausgabe beseitigte. Für diese mühevolle und aufopfernde Arbeit bin ich den Mitarbeitern des Text-Book zu grossem Dank verpflichtet.

Allerdings wurde durch die Betheiligung einer grösseren Anzahl von Autoren, deren Anschauungen in systematischen Fragen nicht immer unter einander und mit denen des Autors der deutschen Ausgabe in Einklang standen, die Einheitlichkeit des Werkes nicht unerheblich gestört und auch der ursprüngliche Umfang verschiedener Abschnitte bedeutend überschritten; allein diese Nachtheile dürften durch die sorgfältigere Durcharbeitung des eigentlichen Stoffes reichlich ausgeglichen sein.

Die Revision der Crinoideen hatte der verstorbene Herr *Charles Wachsmuth*, jene der Asteroideen und Echinoideen Herr *W. Percy Sladen* übernommen. Abgesehen von einigen Abänderungen, welche mehr terminologische als sachliche Fragen betreffen, wurde in diesen Abtheilungen eine weit vollständigere Aufzählung und Characterisierung der fossilen Gattungen durchgeführt, als in der deutschen Ausgabe. Weitergehende Umgestaltung erfuhr die Classe der Bryozoen durch Herrn *E. O. Ulrich*. Die palaeozoischen Formen sind von diesem ausgezeichneten Kenner mit einer Ausführlichkeit behandelt, welche nicht ganz mit der Darstellung anderer Abtheilungen in Einklang steht. Auch die Transferierung der bereits bei den Korallen abgehandelten Chaetetiden und Fistuliporiden zu den Bryozoen und die dadurch veranlasste doppelte Darstellung derselben ist eine Incongruenz, welche sich nur durch die Meinungsverschiedenheit über die zoologische Stellung dieser ausgestorbenen Organismen Entschuldigung lässt.

Eine durchgreifende Umarbeitung haben die Brachiopoden durch Herrn *Charles Schuchert* erfahren. Während sich die deutsche Ausgabe mehr auf die

Werke und Anschauungen von *Thomas Davidson* stützt, folgt die englische Uebersetzung sowohl in der Auffassung der Gattungen und Familien, als auch in den systematischen Principien den neusten Arbeiten von *James Hall*, *J. M. Clarke*, und *C. E. Beecher*. Die systematischen Hauptgruppen sollen hier zugleich entwicklungsgeschichtlichen Phasen entsprechen und das ganze System den Anforderungen des biogenetischen Grundgesetzes genügen. Von ähnlichen Gesichtspunkten wurden auch Professor *Beecher* bei der Bearbeitung der Trilobiten und Professor *Hyatt* bei jener der Cephalopoden geleitet. Es ist mir zweifelhaft, ob die Zeit zu einer durchgreifenden Reform der biologischen Systematik, bei welcher weniger morphologische und vergleichend-anatomische Merkmale, als embryologische und phylogenetische Gesichtspunkte im Vordergrund stehen, jetzt schon gekommen ist ; allein jedenfalls sucht die in Nord America gegenwärtig herrschende Strömung auf einem neuen Weg zur Wahrheit zu gelangen und eine die genealogischen Beziehungen deutlicher wiederspiegelnde Systematik zu erzielen.

Bei den Pelecypoden hat Herr Dr. *W. H. Dall* die durch *Neumayr* eingeführten und in den Grundzügen mit einigen Modificationen angenommenen Gruppen durch seine eigene, auf langjährige Specialuntersuchungen basirte Eintheilung ersetzt. Die Scaphopoden, Amphineuren, Gastropoden und Pteropoden wurden von Herrn Professor *H. A. Pilsbry*, die Crustaceen mit Ausnahme der Trilobiten und einiger anderer Gruppen von Professor *J. S. Kingsley*, und die übrigen Arthropoden von meinem langjährigen Mitarbeiter und Freund Professor *S. H. Scudder* in sachkundigster Weise durchgesehen.

Für den wichtigen Abschnitt der Cephalopoden trägt Herr Professor *Alpheus Hyatt* die Verantwortlichkeit. Hier treten die Differenzen mit der deutschen Ausgabe am auffallendsten zu Tage, vertritt doch dieser Autor am entschiedensten die moderne Richtung in America. Obwohl meine Anschauungen über verschiedene Grundprincipien der Systematik, namentlich über Abgrenzung von Familien, Gattungen und Arten von denen meines amerikanischen Collegen abweichen, so glaubte ich doch einem so hervorragenden Kenner der fossilen Cephalopoden bei der Bearbeitung des von ihm übernommen Abschnittes völlig freie Hand lassen zu müssen. Das TEXT-BOOK ist dadurch um eine werthvolle Originalarbeit bereichert worden, welche viele bis jetzt noch nicht veröffentlichte Thatsachen enthält.

Zu ganz besonderem Dank bin ich dem Herausgeber der englischen Ausgabe Herrn Dr. *C. R. Eastman* verpflichtet. Er hat keine Mühe gescheut, das Werk mit den neusten Ergebnissen der palaeontologischen Forschung in Einklang zu bringen und den Fortgang derselben zu fördern.

DR. KARL A. VON ZITTEL.

MÜNCHEN *im September* 1899.

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INTRODUCTION

DEFINITION AND SCOPE OF PALAEONTOLOGY

Palaeontology (λόγος τῶν παλαιῶν ἔντων) is the science which treats of the life which has existed on the globe during former geological periods. It deals with all questions concerning the properties, classification, relationships, descent, conditions of existence, and the distribution in space and time of the ancient inhabitants of the earth, as well as with those theories of organic and cosmogonic evolution which result from such inquiries.

By fossils, or petrifactions, are understood all remains or traces of plants and animals which have lived before the beginning of the present geological period, and have become preserved in the rocks. The evidence which is in all cases conclusive as to the fossil character of organic remains is the geological age of the formation in which they occur, whereas their mode and state of preservation, or the fact of their belonging to extinct or to still living species, are merely incidental considerations. Although, as a rule, fossils have undergone more or less radical changes during the process of fossilisation, and are usually converted into mineral substances, as the term petrifaction indicates, nevertheless, under exceptionally favourable conditions (as in frozen ground, amber, resin, peat, etc.), plants and animals may be preserved through geological periods in a practically unaltered state. Carcasses of mammoths and rhinoceroses entombed in the frozen mud-cliffs of Siberia, and inclusions of insects, spiders, and plants, in amber are none the less genuine fossils, in spite of their having sustained no trace whatever of mineral infiltration.

A by no means inconsiderable number of plants and animals occurring strictly fossil in Tertiary and Pleistocene formations belong to still living species; while, on the other hand, the remains of forms which have become extinct during historical times (*Rhytina*, *Alca*, *Didus*, *Pezophaps*, etc.) can no more be classed as fossils in the true sense of the word than all such recent organisms as may chance to become buried in deposits now forming under the present prevailing orographic and climatal conditions.

The changes which organic bodies undergo during the process of fossilisation are partly chemical and partly mechanical in their nature.[1] According

[1] *White, Charles A.*, Conditions of preservation of invertebrate fossils. Bull. U.S. Geol. and Geog. Survey Territ., 1880, vol. V. p. 133.
Trabucco, Giac., La Petrificazione. Pavia, 1887.

as certain portions of the original substance are removed, or are replaced atom for atom by foreign matter, the result may be either carbonisation, decomposition, total dissipation, or petrifaction.

Carbonisation is a deoxidising process taking place under water or with limited access of air, and especially common among plants. Fossil wood and other vegetable matter abound in peat, lignite, and bituminous coal, the leaves being transformed into a thin flake of carbon, on which often the finest venation is still discernible. In some cases chitinous animal structures also become carbonised, as in insects, crustaceans, and graptolites.

Decomposition as a rule effectually destroys all organic carbon and nitrogen compounds. With few exceptions, therefore, animals without hard parts, such as worms, infusorians, naked mollusca, most hydrozoa, many anthozoa, and the embryoes of vertebrates, leave no traces behind in the rocks. Horn, hair, chitin, and similar structures are likewise totally destroyed during the fossilisation process, while only under especially favourable conditions, as, for instance, in ice or in frozen soil, muscular and epidermal tissues remain unchanged; or else, through the taking up of lime phosphate in argillaceous and calcareous deposits, undergo a sort of petrifaction, in which the finer structure is but little altered.[1] Even the conservable hard parts of animal bodies are deprived of their organic compounds; bones give up their fats and oils, and the shells of mollusks, echinoderms, and crustaceans lose their pigments and soft substratum. The hard portions, which first become more or less porous through loss of their organic constituents, next suffer the gradual disintegration of their inorganic compounds, and experience lastly either total dissolution, reabsorption, or petrifaction.

Petrifaction.—In this process foreign substances soluble in water (chiefly calcium carbonate and silica, more rarely pyrites, iron oxyhydrate, and other salts) impregnate and completely fill all original cavities as well as those formed subsequently by decay. Chemical metamorphism takes place occasionally, when, owing to the decomposition of certain inorganic constituents, the original molecules become replaced by those of other substances. For instance, we find quartz pseudomorphs after calcareous tests and skeletons, and conversely, calcite pseudomorphs after silica, as in certain sponges.

Wherever the space originally occupied by soft parts, as, for example, the interior of a shell or other hollow body, becomes filled up with infiltrating ooze, while the shell itself or the enclosing wall decays, there is produced a *cast* of the interior, which in most cases (especially where the shell is thin, as in ammonites, brachiopods, certain mollusks, and crustaceans) preserves an exact copy of the original form, and is susceptible of as accurate determination as the real object. Not infrequently fossil organisms leave *molds* or *imprints* of their shells or skeletons—very rarely of their whole bodies—in the rocks. Sometimes, indeed, their presence is indicated merely by *tracks* or *footprints*.

Fossils are often distorted by mechanical agencies, such as faulting, folding, crushing, and other deformations of the country rock. Such cases require especial attention, and due caution must be observed in their determination.

Palaeontology and Biology.—Although the fossil remains of ancient life-forms yield but a fragmentary record of themselves, are almost never

[1] *Reis, Otto,* Ueber Petrificirung der Muskulatur. Arch. mikroskop. Anat., Band XLI.

perfectly preserved, and are usually more or less altered in appearance, yet, on the whole, they readily fit into place in the great framework of the zoological and botanical classifications. Notwithstanding all their differences, they are built on the same general plan as recent organisms, and their identification requires the most careful comparison with nearly related plants and animals. The methods of palaeontological researeh do not differ from those employed by the zoologist and botanist, excepting, of eourse, that the palaeontologist is restricted to those parts alone which are capable of preservation, and must reconstruct the missing soft parts ideally from analogy with recent forms. It is, nevertheless, incumbent on the palaeontologist to obtain all possible information from the material such as it is, aided by every means he can devise; and hence his investigations do not cease with an examination of the external, macroscopic characteristics, but must be extended to the finer microscopic and histological as well. In numerous subdivisions of the animal and vegetable kingdoms, palaeontology has anticipated zoology and botany by important histological diseoveries; in the branch of vertebrate comparative anatomy, for example, through the exhaustive study of conservable hard parts, such as the teeth, skeleton, dermal covering, etc., this science has been elevated to its present high standard chiefly by palaeontologists (Cuvier, Owen, Huxley, H. v. Meyer, Rütimeyer, Marsh, Cope, and others). The principle of correlation of parts, first applied with sueh eminent success by Cuvier, according to which all parts of an organism stand in eertain fixed relationships to one another, so that one part cannot vary without a corresponding variation taking place in the others, is now worked out not only for the whole group of vertebrates, but for invertebrates as well; and its elaboration is such that frequently a single bone, tooth, or plate, a sadly demolished carapace, a shell-fragment, a bit of stem, and the like, is sufficient for us to form a tolerably accurate conception of their former owner. It is therefore clear that in so far as palaeontology has to deal with the study and elassification of fossil organisms, it is no other than a part of zoology, comparative anatomy, and botany, and hence may be very properly divided into *Palaeozoology* and *Palaeobotany*. Palaeontology has astonishingly increased the subject-matter of the two biological sciences, has filled up innumerable gaps in the system, and has infinitely enriched our knowledge of the variety and eomplexity of plant and animal organisation. In almost every class of both kingdoms where preservation is possible, the number of fossil forms considerably exceeds the recent. A natural classification of the Foraminifera, sponges, eorals, echinoderms, mollusks, vertebrates, and of the vascular cryptogams, eycads, and conifers, would be utterly inconceivable without taking palaeontological evidence into account, since in certain classes (brachiopods, eephalopods, reptiles, mammals) the number of extinct fossil forms is ten, a hundred, or even a thousand-fold greater than the living, and this proportion is steadily increasing in favour of palaeontology, since new fossiliferous localities are being discovered almost daily in various parts of the world.

Palaeontology and Geology.—Although as a biological science palaeontology does not differ essentially from botany and zoology, yet its connection with geology is none the less intimate, and consequently it has been cultivated quite as assiduously by geologists as by biologists. The material is brought to light almost wholly by geologists or by geological collectors, who derive it from the stratified rocks of the earth's crust—that is to say, rocks which have been formed by the subaqueous deposition of sediment, or have been built up from

detritus on dry land by the agency of winds. The distribution of fossils among stratified rocks is by no means promiscuous, and neither do all rocks contain the same species; but, on the contrary, each separate stratigraphical-complex, and frequently even single beds and layers, are characterised by certain particular suites of fossils. The older the rock, the more strikingly different from recent organisms are its fossil remains; the younger the formation, the greater is their resemblance. Now, since experience shows that contemporaneous deposits which have been laid down under similar conditions (as, for example, in salt or in fresh water) contain identical or at least very similar fossils, the latter furnish us with an infallible guide, taken together with the local stratigraphic succession, for determining the relative age of a given formation. Furthermore, a knowledge of the fossils occurring in homotaxial deposits enables us to reconstruct the various palaeofaunas and palaeofloras which have existed on our planet at different periods in its history. Having determined the chronological succession of the clastic rocks by means of their superimposition and their characteristic or index-fossils, they may be divided up into still smaller series, each one of which is characterised by a particular assemblage of organic remains. In the main, then, palaeontology is the ultimate foundation of historical geology.

Excluding the oldest metamorphic rocks (gneiss, mica schists, phyllites, etc.) which are destitute of fossils, and concerning whose origin there is still great difference of opinion, the total thickness of the sedimentary rocks amounts to 20,000—30,000 metres. The building up of this prodigious pile of rock must have extended over an inconceivably long time, whose duration cannot even approximately be estimated, since we are without data as to the rate of deposition in former periods, and since the beginning, culmination, and end of geological epochs cannot be correlated with astronomical events.

Since, however, the earth has been inhabited in former times by very different creatures from those now living; since successive palaeofaunas and palaeofloras follow one another everywhere in the same order; and since, furthermore, in certain formations the greater part or even the total number of species appear and disappear in a body, so that one fauna or flora is replaced almost in its entirety by the next following; it is obvious that the sedimentary rocks may be subdivided into a number of longer and shorter time measures, which may be designated by particular names. The beginning and end of such periods (group, system, or formation, series or section, stage, zone, or bed) is usually indicated by local interruptions in the deposition, occasioned by variations in sea-level, volcanic eruptions, or by other causes; and such disturbances are usually accompanied by changes in the flora and fauna. The now generally accepted subdivision of the secondary rocks is represented in the table on page 5, in which it should be noted that only the first three columns are of universal significance, while the last two apply only to European conditions.

The rocks of the *Archaean Group* amount to 40,000—60,000 metres in thickness. They belong to the oldest and longest period in the history of our planet, and are remarkable for their schistose and crystalline structure, as well as for the total absence of fossils. In order of stratigraphy, gneiss comprises for the most part the oldest, mica, chlorite, and talc-schists the middle, and phyllites (primitive schists) the youngest division of this group. The so-

Eras	Periods			Epochs	
Cenozoic Group	Quarternary System		Alluvium	Recent Deposits	
			Diluvium (Pleistocene)	Postglacial Series Glacial ,, Preglacial ,,	
	Tertiary System	Neogene	Pliocene	Sicilian Series Astian ,,	(Sicilien) (Astien)
			Miocene	Pontian Series Sarmatian ,, Tortonian ,, Helvetian ,, Burdigalian Series	(Pontien) (Sarmatien) (Tortonien) (Helvetien) (Burdigalien)
		Eogene (Palaeogene)	Oligocene	Aquitanian Series Tongrian ,,	(Aquitanien) (Tongrien)
			Eocene	Ligurian Series Bartonian ,, Parisian ,, Suessonian ,, Thanetian ,,	(Ligurien) (Bartonien) (Lutetien) (Suessonien) (Thanetien)
Mesozoic Group	Cretaceous System		Upper Cretaceous	Danian Series Senonian ,, Turonian ,, Cenomanian Series	(Danien) (Senonien) (Turonien) (Cenomanien)
			Lower Cretaceous	Gault Series Aptian and Urgonian Series Barremian Series Neocomian ,,	(Albien) (Aptien, Urgonien) (Barrémien) (Neocomien)
	Jurassic System		Upper Jurassic (Malm)	Tithonian and Portland Series Kimmeridgian ,, Oxfordian ,, Kellaway ,,	(Portlandien) (Kimmeridgien) (Oxfordien) (Callovien)
			Middle Jurassic (Dogger)	Bath or Great Oolite Series Bajeux or Inferior Oolite Series	(Bathonien) (Bajocien)
			Lower Jurassic (Lias)	Toarcian Series Charmouthian Series Sinemurian ,, Hettangian ,,	(Toarcien) (Liasien) (Sinemurien) (Hettangien)
	Triassic System		Upper Triassic (Keuper)	Rhaetic Series Carniolan ,, Norian ,,	(Rhaetien) (Carnien) (Norien)
			Middle Triassic (Muschelkalk)	Ladinian Series Virglorian ,,	(Ladinien) (Virglorien)
			Lower Triassic (Bunter Sandstein)	Werfenian Series	(Werfenien, Vosgien)
Palaeozoic Group	Permian System (Dyas)		Zechstein Rothliegendes	Thuringian Series Punjabian ,, Autunian ,,	(Thuringien) (Punjabien) (Autunien)
	Carboniferous System		Coal Measures	Uralian Series Muscovian ,,	(Uralien) (Moscovien)
			Carboniferous Limestone (Culm)	Dinantian Series	(Dinantien)
	Devonian System		Upper Devonian	Famennian Series Frasnian ,, Givetian ,,	(Famennien) (Frasnien) (Givetien)
			Middle Devonian	Eifelian Series	(Eifelien)
			Lower Devonian	Coblenzian Series Gedinnian ,,	(Coblenzien) (Gedinnien)
	Silurian System		Silurian	Ludlow Series Wenlock ,, Upper Llandovery Series	(Gothlandien)
			Ordovician (Lower Silurian)	Bala or Caradoc Series Llandello ,, Arenig ,,	(Ordovicien)
	Cambrian System		Upper Cambrian	Tremadoc Series Festiniog ,,	(Potsdamien)
			Middle Cambrian	Menevian Series	(Acadien)
			Lower Cambrian	Harlech Series	(Georgien)
Archaean Group	Primitive Schist System Gneiss System		Phyllite (Primitive Schists, Mica and Chlorite Schists, etc.) Gneiss	Precambrian Series	(Algonkien)

called fossil organism, *Eozoon*, occurring in gneiss, has been proved to be of inorganic nature.

The *Palaeozoic* or *Primary Group* comprises the Cambrian, Ordovician, Silurian, Devonian, Carboniferous, and Permian systems, each of which is made up of a great number of series, stages, and zones. In the Cambrian crustaceans (trilobites), mollusks and worms predominate, associated with a few Pelmatozoa, coelenterates, sponges, and poorly preserved algae. In the Silurian system all classes of the animal kingdom are represented with the exception of amphibians, reptiles, birds, and mammals, while the flora still consists of algae. Marine invertebrates are very abundant, especially crustaceans, mollusks, echinoderms, and coelenterates, while only a few fragmentary fish-remains indicate the presence of vertebrates. All the species, and nearly all the genera, have since become extinct, and belong for the most part to extinct families and orders. During the Devonian, Carboniferous, and Permian systems, the same classes of animals continue as a body, but are represented by totally different families and genera. Fishes develop a great variety of forms in the Devonian, amphibians (*Stegocephalia*) make their appearance in the Carboniferous, and reptiles in the Permian. The flora consists chiefly of vascular cryptogams, together with a few conifers and cycads.

The *Mesozoic Group* comprises three systems—the Triassic, Jurassic, and Cretaceous. Many of the widely distributed Palaeozoic types (*Tetracoralla, Graptolites, Crinoids, Cystids, Blastoids, Brachiopods, Trilobites*) have either wholly or in greater part disappeared, while others (*Cephalopods, Lamellibranchs, Sea-urchins*) are replaced by very different genera and families. Vertebrates are remarkable for the gigantic size attained by amphibians (*Labyrinthodonta*) and many reptiles, as well as for the wonderful variety of the latter. Birds appear for the first time in the Upper Jurassic (*Archaeopteryx*), and mammals towards the close of the Triassic, being represented by diminutive, probably marsupial types. During the Triassic and Jurassic periods, vascular cryptogams, conifers, and cycads remain the dominant plant forms, dicotyledons not occurring until the middle Cretaceous.

The *Cenozoic Group* comprises the Tertiary and Post-Tertiary or Quaternary systems. Among the invertebrates, ammonites, belemnites, Rudistae, and most of the Crinoidea have now passed away. Amphibians and reptiles have greatly declined, and, like the invertebrates, are represented by still living orders. On the other hand, birds, and most particularly mammals, attain a wide distribution; the latter class branches out in such manifold variety, and experiences such rapid development during Cenozoic time, that it alone furnishes us with the principal index-fossils of this era. From now on the flora consists chiefly of dicotyledonous plants.

Palaeontology and Physical Geography.—Not only do fossils constitute the very foundation of historical geology, but they furnish us in addition with invaluable information respecting the origin of the rocks in which they occur, the former distribution of land and water, climatal conditions, and the laws of geographical distribution that have prevailed in former periods. By means of analogy with recent species we are able in most cases readily to determine whether fossil forms pertain to land, fresh, brackish, or salt water species, whence it is apparent under what conditions the strata were deposited. The distribution of marine and fresh-water formations helps us to certain conclusions respecting the extent of former

seas and land areas. Deep-sea, shallow water, and littoral deposits are readily distinguishable by means of their fossil organisms. By fossils, also, even the climatal conditions of former periods are recorded with great fidelity. The luxurious and uniform development of cryptogams over the face of the globe during Carboniferous time presupposes a warm, moist climate, little varying with latitude; tropical dicotyledons occurring in the Cretaceous and Tertiary deposits of Greenland, or coral-reefs extending into high latitudes during the Palaeozoic era, prove with equal certainty the prevalence of a milder climate and higher oceanic temperature in earlier times; while again, the remains of reindeer, the lemming, musk-ox, polar fox, and other arctic animals in the diluvium of Central Europe testify to a period of glaciation with reduced mean annual temperature.

The geographical distribution of fossil organisms proves that the regions and provinces occupied by recent plants and animals are to a certain extent identical with those existing in the Tertiary, and that life has been subject to the same distributional laws in the past as in the present. Nearly all recent forms are the obvious descendants of extinct creatures which formerly occupied the same region. For example, the fossil mammals, birds, and reptiles of Diluvial time in Europe, Asia, Australia, North and South America, are scarcely distinguishable from forms now inhabiting the same continents. The old ancestral homes of marsupials and edentates were perpetuated in Australia and South America until as recently as the Diluvial epoch, and during the Tertiary, Europe, Asia, and America formed but a single zoological province, inhabited by the ancestors of forms now living in the northern hemisphere. An understanding of the physical conditions which have governed the perpetuation of recent plants and animals in their respective provinces (*succession of similar types*) would be utterly impossible without a knowledge of their distribution in former times. In like manner, our knowledge of the distribution of land and water, of the climatal conditions, oceanic currents, etc., of earlier periods depends chiefly upon evidence derived from fossils.

Palaeontology and Embryology (*Ontogeny*).—To trace living plants and animals through all stages of growth from the egg upward to maturity, and thence on to final dissolution, is the task of Embryology or Ontogeny. At the present moment, botanists and zoologists are devoting their most scrutinising attention to embryological investigations, which latter accordingly exert a powerful influence on the progress of biology, and particularly on the classification. The fact that every individual, species, and genus of a whole group of plants and animals passes through nearly the same course of development, at least in the primary stages, and that all embryoes belonging to a given order or class resemble one another so closely, up to a certain stage, that they cannot be told apart, has revealed unexpected affinities among forms differing very considerably in the adult stage. Cirripedes, for example, which were formerly mistaken for shell-bearing mollusks, develop from the same Nauplius-larvae as the Copepoda, Phyllopoda, and Ostracoda, although the mature individuals belonging to these orders of crustaceans possess but little common resemblance. Likewise, the whole group of vertebrate embryoes can hardly be distinguished from one another in the earliest stages, and only very gradually assume the characteristic features pertaining to class and order.

The results of embryological inquiry have a most important bearing on palaeontology. Numerous fossil forms are known, which, in comparison with recent related organisms, exhibit embryonic, or at least larval or adolescent characteristics. Examples of such persistent *embryonic types* are especially common in vertebrates, for the reason that here the skeleton becomes ossified very early in life, and hence the immature stages of the recent can be directly compared with adult fossil forms. Now, observation has shown that in most of the older fossil fishes and reptiles, the vertebral column never passed beyond an embryonic stage, but remained in a cartilaginous or incompletely ossified condition through life. The Palaeozoic amphibians (*Stegocephalia*) probably breathed by means of both gills and lungs throughout life, whereas most recent amphibians lose their gills comparatively early (*Caducibranchia*), and breathe wholly by lungs. Many fossil reptiles and mammals retain certain skeletal peculiarities permanently, while allied recent forms exhibit them only in embryonic stages. The construction and shape of the skull in most of the older fossil reptiles and mammals closely corresponds with that in embryoes of recent related types. In the oldest fossil artiodactyls the palm-bones are all completely separated, while in recent ruminants this division continues only during the embryonic stage, being followed by a fusion of the two median metapodals, together with a reduction of the laterals. Among invertebrates, also, fossil embryonic types are by no means uncommon. The Palaeozoic *Belinuridae* find their counterpart in the larvae of the common *Limulus;* many fossil sea-urchins are characterised by linear ambulacra, while recent related forms, although developing petaloid radii in the adult stage, pass through the linear phase during adolescence. Many fossil crinoids before maturity resemble the living genus *Antedon;* and, according to Jackson, recent oysters and Pectens exhibit in their nepionic stages certain characters peculiar to Palaeozoic genera of mollusks.

The so-called fossil *generalised* or *comprehensive types*, which unite in one and the same form characters which, in geologically later, or recent descendants, have become distributed among different genera and families, are in reality merely adolescent or immature types which have stopped short of the higher differentiation attained by their descendants. Generalised types always precede more highly specialised; and properties that were originally distributive among older forms are never reunited in geologically younger species or genera. Trilobites, amphibians, and reptiles of the Palaeozoic and Mesozoic eras, and early Tertiary mammals belong almost exclusively to the category of generalised types.

In certain groups of vertebrates, and especially of mammals (*Ungulata, Carnivora*), the chronological succession of genera is so closely paralleled by the successive stages of development in the life-history of their descendants, that to a certain extent the ontogeny of the individual is a representment of a long chronological series of fossil forms. This truth furnishes a strong foundation for the *biogenetic law*, enunciated in various terms by Geoffroy St. Hilaire, Serres, Meckel, Fritz Müller, and others, and recently more precisely formulated by Haeckel, as follows:—The developmental history, or ontogeny of an individual is merely a short and simplified repetition or recapitulation of the slow (perhaps extending over thousands of years) process of evolution of the species and of the whole branch.

The biogenetic law has since been found to hold true not only for verte-

brates, but also for invertebrates, including even totally extinct types. In ammonites, for instance, the primary or innermost whorls always differ from the outer in their greater simplicity of suture, and in their lesser ornamentation. Very often a similarity is observable with geologically older forms; and it is a well-known fact that all ammonites pass through early stages which resemble, at least so far as chambering of the shell is concerned, Palaeozoic goniatites. A comparison of the inner whorls of an ammonite with its corresponding goniatitic form, or with older ammonites, seldom fails to reveal ties of kinship not otherwise discernible. Beecher has shown that nearly every stage in the growth of arm-supports in recent brachiopods corresponds to some fossil genus; and further, that the chronological succession of the latter is to a certain degree identical with the successive ontogenetic stages of recent forms.

The relation of so-called *rudimentary organs* occurring in recent forms to those of the allied predecessors of the latter is of particular significance. By rudimentary organs are meant certain structures (as, for example, limbs, parts of limbs, organs of sense, respiration, digestion, reproduction, etc.), which are still indicated by dwarfed remains, but whose physiological functions, and hence their utility to the organism, have wholly disappeared. Rudimentary organs are, as a rule, either normally developed in an embryonic stage, or at least more strongly than in the adult individual, owing to a process of *degeneration*, or retrogressive development. The fossil progenitors of forms possessing rudimentary organs are almost always characterised by a full development of the respective parts. The lateral metacarpals and metatarsals in the horse and most ruminants, for example, are indicated only by rudimentary side-splints; but in an embryonic stage they are much more strongly developed, and in related fossil forms they occur as normal bones, carrying toes like the other metapodals, and serving for locomotion and support. The wrist and metacarpal bones in birds have also suffered degeneration, as is evident from a comparison with embryoes and with older forms (*Archaeopteryx*), which exhibit a much higher development. In like manner, the teeth of birds have also become degenerated. In only a few forms (parrots) are indications of dental ridges discernible during embryonic stages; but in all known Mesozoic birds the teeth are well developed and remain functional throughout life. Similarly, teeth are developed during embryonic stages in the baleen whale, but subsequently become atrophied; while in the older fossil Cetacea teeth are always present. Other instances of this nature are to be met with in great profusion, both among vertebrates and invertebrates.

The biogenetic law is, however, not infrequently obscured, for the reason that two closely related forms may not develop in exactly the same manner; embryoes of the one type may be affected by peculiar accelerating impulses which are not shared by those of the other, and in consequence the first may pass through certain stages very rapidly, or may even omit them altogether. In this way the historical or palingenetic record contained in the growth of every individual may be to a large extent suppressed or rendered unintelligible; and this phenomenon of inexact parallelism (*coenogenesis*) is especially common in highly differentiated types, where the embryo passes through a multitude of phases.

Palaeontology and Phylogeny.—While conceding that by means of

embryological investigations zoologists and botanists are able to trace out the gradual development and differentiation of an organism through all its various stages, and thereupon to construct a tree of descent (*phylogeny*) founded upon the successive phases of growth, nevertheless such hypothetical genealogies can only be relied upon as truthful when they are substantiated by palaeontological facts. And only in cases where the different ontogenetic stages are represented by corresponding fossil embryonic or generalised types, which appear in the same chronological order, and clothe the suppositious ancestral tree with real forms, can the truthfulness of the latter be said to have been established. This requirement palaeontology is from the nature of things unable to satisfy except in a few instances; but a multitude of other facts, however, testifies to the blood-kinship between morphologically similar fossil and recent organisms, and points to the direct descent of the younger from the older forms.

Geology proves conclusively that of the numerous floras and faunas which lie buried in the rocks, those which are most nearly of the same geological age bear the greatest resemblance to each other. It often happens that species and genera occurring in a given formation reappear in the next following with scarcely any perceptible changes, so that the doctrine of the gradual transformation and transmutation of older forms is irresistibly forced upon one, while the faunas and floras of later periods assert themselves as the obvious descendants of the more ancient. Other weighty evidence for the progressive evolution of organisms is afforded by fossil *transitional series*, of which a considerable number are known to us, notwithstanding the imperfection of the palaeontological record. By transitional series are meant a greater or lesser number of similar forms occurring through several successive horizons, and constituting a practically unbroken morphic chain. Oftentimes, indeed, the differences between individuals belonging to different periods are so slight that we can hardly assign to them the value of a variety. But let a number of such mutations occur in succession, the end-members of the series become finally so divergent as to constitute distinct species and genera. The most striking and most numerous examples of transitional series naturally occur in types peculiarly well fitted for preservation, such as mollusks, brachiopods, sea-urchins, corals, and vertebrates. Particularly remarkable among mollusks are the closely linked transitional series in ammonites. Among vertebrates transmutation proceeded far more rapidly than among invertebrates, and accordingly, the successive members of a series are usually so divergent as to require their assignment to separate genera.

With increasing abundance of palaeontological material, the more numerous and more complete are the series of intermediate forms which are brought to light. But the more extended our knowledge of transitional series, the greater is the difficulty we encounter in defining our *conception of species*. While the older disciples of the Linnaean and Cuvierian schools contended that each individual species was created with a certain definite sum of fixed characters, and remained incapable of any extensive modifications; on the other hand, those holding to the theory of descent, evolution, or transmutation, look upon varieties, species, subgenera, genera, families, orders, classes, and subkingdoms as distinctions of merely transient importance, corresponding to the state of our information at the present time; it being assumed that by means of gradual transmutation during the course of ages all organisms

have become evolved from a single primitive cell, or from a few primitive types.

According to the Linné-Cuvier doctrine, a species is composed of individuals which are directly descended from one another, or from common ancestors, and which resemble their progenitors as much as they resemble each other. Members of one and the same species interbreed, while individuals belonging to different species do not cross, or when they do, produce infertile or imperfectly fertile offspring.

According to the theory of descent, no sharp specific distinctions can be drawn, but all individuals are assigned to the same species which possess a number of essential properties in common, and which are not connected on all sides with neighbouring groups by means of intermediate types. It is plain that this definition is open to considerable laxity of interpretation, and inasmuch as the direct descent of individuals belonging to a given species cannot always (in palaeontology never) be determined on experimental grounds, systematists are rarely fully agreed in regard to the limitations of species, genera, and families.

The doctrine of the invariability of species received powerful support from the cataclysmic theory of Cuvier, which maintained that each period in the earth's history is marked by distinctively characteristic faunas and floras; that no species is common to two successive periods; that tremendous convulsions of nature (*cataclysms*) occurred at the close of each cycle, and annihilated the whole organic world; and that by means of special creative acts, the renovated earth became time and again populated with new animals and plants which bore absolutely no connection either with previous or with subsequently introduced types.

Cuvier's cataclysmic theory may be regarded at the present day as completely overthrown, inasmuch as the modern school of geology, following the leadership of Sir Charles Lyell, has demonstrated conclusively that the earth has proceeded from one stage to another during the course of its development only with the utmost slowness; that the same forces and laws which regulate the world of to-day have operated likewise in primeval times; and that geological periods are by no means abruptly set off from one another, but, on the contrary, are linked together by innumerable transitional stages.

The theory of the descendant origin of organic forms, which was advanced as early as 1802 by J. B. Lamarck and Geoffroy St. Hilaire, and was supported by Göthe, Oken, and Meckel in Germany, kept winning continually more and more adherents, yet it was not until the latter half of the present century that its universal significance was insisted on by Charles Darwin and his school.

Palaeontology, as already remarked, contributes a great deal of extremely weighty evidence in favour of the theory of descent; the series of intermediate forms, often traceable through several successive formations; the presence of embryonic and generalised types; the parallelism between ontogeny and the chronological succession of related fossil forms; the similarity between floras and faunas of approximately the same age; the correspondence in the geographical distribution of recent organisms with that of their progenitors; and a host of other facts are explicable only by means of the theory of descent.

The *causes* of variation and transmutation were attributed by Lamarck chiefly to the use and disuse of organs; secondly, to the effect of changes in external conditions; and lastly, to a supposed resident tendency toward variation

and perfection existing in each individual. According to Lamarck, new properties brought about by these influences are transmitted to descendants through inheritance, and become permanently established in the race. Geoffroy St. Hilaire maintained the same principles on the whole, but ascribed the chief causes of variation of species to the influence of environment.

The Darwinian theory of natural selection is based upon the property common to all organisms of acquiring ancestral characteristics through heredity, and of transmitting them in turn to their progeny; and also on the adaptability of organisms to particular external conditions, by means of which variations are brought about. Since in the struggle for existence only those individuals which are the best adapted—that is to say, those possessing the most advantageous modifications—survive, nature is continually exercising, according to Darwin, a most rigorous selection which operates toward the increase and perfection of useful variations. Through the constant accumulation of originally slight yet serviceable modifications, and through the perpetual transmission of the same from one generation to another, there are produced first different varieties, then species, and eventually genera, families, and orders. The zoological and botanical classifications are, according to Darwin, merely an expression of genealogical facts, exhibiting the remoter and closer ties of consanguinity which exist among different organic forms.

Darwin's explanation of the origin of species through the agency of natural selection found in Wallace, Huxley, Haeckel, and others, zealous and ingenious supporters, while on other sides it encountered vehement opposition. M. Wagner regarded free intercrossing as an insurmountable obstacle to the establishment of new modifications, and contended that the isolation of a few individuals, a condition which would occur most frequently during migrations, was a necessary postulate in accounting for the origin of each new variety or species. Bronn, Nägeli, and A. Braun raised the objection to Darwin's theory of natural selection that many organs are entirely useless to the individual, and therefore natural selection, which depends upon the principle of utility, could neither have produced such organs nor could have modified them in any way. Nägeli assumed that, in addition to natural selection, a certain resident tendency toward perfection, inherent in every individual, takes part in conditioning the growth of morphological characters. Every variation brought about by external or internal agencies is at once in the nature of a differentiation, a step forward in the division of labour, and consequently an advancement.

Weismann endeavoured in a similar manner to supplement Darwin's theory of selection by his hypothesis of the continuity of germ-plasm. According to Weismann, germ-matter is of itself capable of producing all variations that are useful to an organism. Only that which exists in the original plasm or in the sexual elements as embryonic rudiments can be transmitted to offspring and become further acted upon and developed by natural selection, according to Weismann's theory. The continuity, that is to say, the perpetual transmission of a portion of the germ-plasm from parents to offspring, forms a necessary postulate to the theory of descent. In opposition to Weismann, who attributes only a subordinate influence to the action of physical environment as a cause of variations, and who particularly denies the inheritance of acquired characters, stands the Neo-Lamarckian school (represented by Herbert Spencer, Cope, Hyatt, Osborn, Semper, Claus, Roux, and others), which ranges itself more and more on the side of Lamarckian ideas, and ascribes to the use

and disuse of organs, and to external conditions, a very considerable influence in effecting the transmutation of organic forms. While, on the one hand, Semper, Locard, and Clessin undertake to prove the direct action of environment on mollusks in a number of instances, and Schmankewitz confidently asserts that the transformations in *Artemia* are induced by changes in the saltness of the water; on the other hand, Cope, Osborn, Roux, and others, emphasise the effect of use and disuse, and abundance or scantiness of food-supply. Adequate nourishment and exercise increase the development of a given organ, while physical conditions determine its form. Since like causes produce like effects in the animate as well as in the inanimate world, it is obvious that similar organs must be developed in a variety of plant and animal forms wherever they are subjected to similar external conditions, and especially to the same physical agencies. A convenient explanation is thus found for the phenomena of parallelism, or recurring "common types of structure," which are in nowise related to one another by inheritance. The analogous swimming-organs of fishes, ichthyosaurians, and whales, or the analogous limb-structure in long-legged ruminants, the horse, elephant, and carnivora, are due to adaptation to external conditions and to use; the same explanation also accounts for the like form of sternum in bats, birds, and *Pterosauria*, or for the spindle-shaped body characteristic of most rapid-swimming fishes, reptiles, and aquatic mammals, or for the similar form of jaw possessed by marsupials and various orders of *Placentalia*. These are all instances of parallelism, in which it often happens that two fundamentally different forms acquire the same outward shape, or become provided with similar or analogous organs. *Kinetogenesis*, or the process of a gradual transformation of parts, especially parts belonging to the internal skeleton, skull, and limbs, is very ingeniously interpreted by Cope as having been accomplished in mammals through the agency of mechanical conditions, use, and food. The same author has also traced out the different stages of development in fossil genera as exemplified by numerous series of intermediate forms.

Life-Period and Extinction of Species.—Observation shows that different organisms are by no means equally susceptible to impulses received from the outer world. Many fossil genera remain almost wholly unchanged throughout a number of formations (*Foraminifera*, *Cidaris*, *Nautilus*, *Lingula*, *Terebratula*, *Insectivora*), and hence may be designated as *persistent* or *conservative types*, in contradistinction to *variable types*. The latter pass through rapid changes at the beginning of their career, develop a great variety of forms, and send out branches and off-shoots in all directions up to a certain point; they may then die out after a comparatively short period of ascendency (*Nummulites*, *Graptolites*, *Cystids*, *Blastoids*, *Tetracoralla*, *Palechinoidea*, *Trilobitae*, *Rudistae*, *Ichthyosauria*, *Pterosauria*, *Dinosauria*, *Amblypoda*, *Toxodontia*, etc.), or in some cases may even continue on to the present day with undiminished vitality (*Spatangidae*, *Clypeastridae*, many land and fresh-water mollusks, crabs, lizards, snakes, ruminants, apes). Not infrequently types that were primitively variable pass over gradually into persistent; their power of adaptation dwindles, they grow less plastic, become incapable of sending off new varieties, species, or genera, and as the less vigorous of their number become worsted one after another, they finally stand out like curious, isolated relics of antiquity (*Pentacrinus*, *Hatteria*, *Tapirus*, *Equus*, etc.) in the midst of subsequently remodelled surroundings. A one-sided development in a certain direction, excessive size, abnormal

(*hypertrophic*) peculiarities, or too high specialisation of organs, is as a rule injurious to the form and leads usually to its extermination. Many groups remarkable for their extreme differentiation (*Dinosauria*, *Pterosauria*, *Amblypoda*, *Toxodontia*, etc.) have become extinct probably for this reason, since, having advanced so far in a single limited direction, adaptation in other directions was no longer possible.

Persistent types seldom produce a large number of species during a single geological period; types that start up suddenly and proceed to vary rapidly as a rule soon die out; while groups that develop slowly and steadily usually contain in their growth the promise of great longevity.

For the extinction of many plants (*Sigillaria*, *Lepidodendron*, *Filices*) and animals (*Blastoids*, *Tetracoralla*, *Trilobites*, *Ammonites*, *Rudistae*, *Ichthyosauria*, etc.) of former periods no adequate explanation has as yet been found. Changes in external conditions, especially such as regards the distribution of land and water, climatal conditions, saltness of the water, volcanic eruptions, paucity of food-supply, and the encroachments of natural enemies, may have led in many instances to the extinction of certain forms, but such conjectures signally fail to account for the disappearance of an entire species or particular group of organisms. Oftentimes extinction seems to have been caused merely by superannuation. Long-lived forms belong for the most part to persistent types whose range of species is limited. Their reproductive functions have declined, and like an individual in its dotage, they evince all the symptoms of decrepitude and old age. Darwin attributes the extinction of less well-adapted organisms to the struggle for existence; but since, according to the theory of natural selection, new species arise only with extreme slowness by means of the gradual accumulation of useful variations, and since in like manner their less successful competitors are only very gradually crowded out, we should expect to find in the rocks, supposing that the palaeontological record were in any degree perfect, all manner of extinct intermediate forms, and we should be able, at least for those groups especially liable to conservation, to build up complete ancestral trees. But as observation shows, not only do most plants and animals now living in a wild state adhere to their peculiar characteristics with great tenacity, exhibiting barely appreciable changes even in the course of hundreds or thousands of years, but, furthermore, fossil species remain within the limits of a single geological period fairly constant. With the beginning of a new epoch or period, however, which is usually indicated in the rocks by petrographical changes, a greater or lesser number of species either entirely disappears, or is replaced by closely related, but at the same time more or less different forms. Obviously, therefore, there have been periods when the process of transformation and the weeding out of organisms were greatly accelerated, and following upon these reconstructive periods long intervals of repose have ensued, during which intervals species have adhered to their characteristic forms with but little variation. The fact that evolution has advanced by occasional bounds or leaps stands, however, in nowise contradictory to the theory of descent.

The whole animate community at any point on the earth's surface rests normally in a state of equilibrium, the balance being maintained by the concerted action of all ranks and members of society. For the preservation of this balance nature practises a most rigid domestic economy. Every plant depends upon particular conditions of soil, food, temperature, moisture, and

other requisites for its support; and these conditions govern its distribution and increase in the last degree. Every plant controls the destiny of all animals subsisting upon it; their numbers multiply with its increase, and wane with its decrease. The fate of these creatures determines that of their natural enemies, who stand in similar relationships to still remoter circles; and hence no form can overstride the bounds set for it by the general balance without disturbing the whole general system of economy. Let the flora or fauna of a given region become altered by the extinction of a number of species, or by the introduction of new and more powerful competitors, the balance is immediately upset. In the first instance vacant places must be filled up, and in the second, room must be made for the newcomers at the expense of the settled community. Thus, wherever climatal, orographic, or other changes are instrumental in bringing about the extermination of large numbers of plants and animals during the lapse of a geological period, an inequilibrium must necessarily result. But thereupon the struggle for existence is waged with unwonted severity among the survivors, until finally a new state of equilibrium is attained, and a pause in the formation of new species ensues.

The whole course of evolution in the organic world during past geological periods indicates not only definite progression in all branches of the animal and vegetable kingdoms up to their present state, but also an *advance toward perfection*. Granting that the theory of descent is true, and that all organisms have developed from a single primitive cell, or from a few primitive ground-types, then every new growth and differentiation must stand for improvement and progress, leading gradually to the development of more or less highly specialised organs, and to a division of labour in their physiological functions; the higher the degree in which this is manifested, and the more conformably to apparent purpose and utility that each organ fulfils its functions, the more perfect is the organism, as we conventionally term it. Evolution in the organic world has not advanced in a simple, straightforward direction, but in an exceedingly complicated and circuitous. The biological systems, accordingly, do not suggest to us the similitude of a ladder with its numerous rounds, but rather that of an enormously ramifying tree, whose topmost twigs represent the youngest, and, on the whole, the most perfect forms of every branch. The root, trunk, and a goodly portion of the upper limbs lie buried in the earth; and only the ultimate green shoots, the last and most highly differentiated members of long ancestral lines, blossom forth in the world of to-day.[1]

[1] [In connection with the two preceding topics, see a paper by the author, read before the International Congress of Geologists, 1894, on "Palaeontology and the Biogenetic Law" (reprinted in Natural Science, vol. VI., May 1895).

On the terminology of evolution in general, see *A. Hyatt*, "Bioplastology and the Related Branches of Biologic Research" (Proc. Bost. Soc. Nat. Hist. vol. XXVI., 1893). Abstract of same in Zoolog. Anzeiger, No. 405, 1892. Other terms employed in the foregoing are introduced and explained by Cope in his "Origin of the Fittest," 1887, and in various articles in the American Naturalist.—TRANS.]

Outline Classification of the Animal Kingdom.

Sub-Kingdoms.	Sub-Branches.	Classes.
I. PROTOZOA		1. *Rhizopoda.* 2. *Flagellata.*[1] 3. *Infusoria.*[1] 4. *Gregarina.*[1]
II. COELENTERATA	I. Porifera	1. *Spongiae.*
	II. Cnidaria	1. *Anthozoa.* 2. *Hydrozoa.*
III. ECHINODERMATA	I. Pelmatozoa	1. *Crinoidea.* 2. *Cystoidea.* 3. *Blastoidea.*
	II. Asterozoa	1. *Ophiuroidea.* 2. *Asteroidea.*
	III. Echinozoa	1. *Echinoidea.* 2. *Holothurioidea.*
IV. VERMES		1. *Platyhelminthes.*[1] 2. *Nemathelminthes.* 3. *Gephyrea.* 4. *Rotifera.*[1] 5. *Annelida.*
V. MOLLUSCOIDEA		1. *Bryozoa.* 2. *Brachiopoda.*
VI. MOLLUSCA		1. *Lamellibranchiata.* 2. *Scaphopoda.* 3. *Amphineura.* 4. *Gastropoda.* 5. *Cephalopoda.*
VII. ARTHROPODA	I. Branchiata	1. *Crustacea.*
	II. Tracheata	1. *Myriopoda.* 2. *Arachnoidea.* 3. *Insecta.*
VIII. VERTEBRATA		1. *Pisces.* 2. *Amphibia.* 3. *Reptilia.* 4. *Aves.* 5. *Mammalia.*

[1] Unknown in the fossil state.

Sub-Kingdom I. PROTOZOA

Protozoa are unicellular organisms, with bodies consisting of sarcode (protoplasm), usually very minute, frequently microscopic in size, and without differentiated tissues or organs. They are water-inhabitants, take in nourishing matter either at any point on the periphery of the body whatsoever, or through a so-called mouth (*cytostome*), and reject the undigested portions either from any part of the body whatsoever, or from a definite point called the anal aperture (*cytopyge*). The contractile sarcode almost invariably contains one or more nuclei, and exhibits considerable diversity of structure and differentiation. Locomotion is accomplished by means of vibratile cilia, flagella, pseudopodia, or irregular processes of the periphery. Reproduction takes place by means of budding or self-division, which latter process is often preceded by a temporary coalescence (*conjugation*) of two individuals. Protozoa are divided into four classes: *Rhizopoda*, *Flagellata*, *Infusoria*, and *Gregarina* (*Sporozoa*), of which only the first class is represented in the fossil state.

Class 1. RHIZOPODA.

Body-substance composed of richly granulated, jelly-like sarcode, which alternately protrudes, retracts, and again coalesces with irregular, finger-like, or thread-like processes called pseudopodia.

Rhizopods have been so named on account of the property they possess of protruding pseudopodia from the periphery of the body. Although serving as a means of locomotion and for the taking up of nutritive matter, the pseudopodia represent no permanent organs, since they are protruded only for the passing occasion, and disappear again as they coalesce with the main body of sarcode. The pseudopodia often exhibit protoplasmic streaming, and occasionally interlace so as to form networks. Rhizopods usually secrete calcareous, silicious, or chitinous tests, or build silicious skeletons of exceeding great diversity of form. Enormous deposits are built up by their accumulation on the sea-floor, and numerous strata of marine origin are largely composed of their remains.

Four orders of Rhizopods are recognised: *Foraminifera*, *Radiolaria*, *Amœbina*,[2] and *Heliozoa*; of these only the first two have parts capable of preservation.

[1] *Bütschli, O.*, Protozoen in Bronn's Classen und Ordnungen des Thierreichs, 1880-1889.

[2] To the *Amœbina*, Huxley and Haeckel formerly assigned the so-called *Bathybius*, a reticulated jelly-like substance composed of anastomosing strands, and occurring at great depths in the Atlantic Ocean. Wyville Thomson and Moebius regarded it as a precipitate of calcium sulphate.

Order 1. FORAMINIFERA. d'Orbigny.[1]

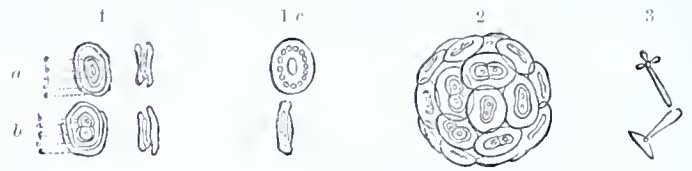
(*Polythalamia*, Breyn; *Thalamophora*, Hertwig.)

Rhizopoda with slender, thread-like, or band-like, frequently anastomosing pseudopodia, and usually with a calcareous, more rarely with an arenaceous or chitinous test.

The scarcely differentiated, richly granulated sarcode body of the Foraminifera usually contains a contractile vacuole, and is enclosed by a shell or test which is almost invariably calcareous in composition, although in some cases it may be of a silicious or even chitinous nature, and which, as a rule, is divided into chambers by interior partitions or septa. The sarcode communicates with the exterior either by means of a single large aperture (oral or general aperture) situated at one extremity of the test, or by means of innumerable fine pores (foramina) which perforate the shell. Through these openings the sarcode emits usually long, filiform, net-like anastomosing pseudopodia, in which often active granular currents are discernible.

Only a few forms secreting chitinous tests (*Gromia*) are fresh-water inhabitants; the rest are marine in habit. Foraminifera are usually so small in size that, although perceptible to the naked eye, they can barely be discriminated as separate individuals. Certain exceptionally large forms (*Nummulites*) attain a diameter of four or five centimetres.

intermingled with decomposed organic matter. In deep-sea ooze, which consists chiefly of lime carbonate, as well as in *Bathybius*, great quantities of minute calcareous bodies of various shapes are found, such as also occur as an essential constituent of chalk, marls, and most marine limestones belonging to older geological periods (cf. *C. W. Gümbel*, Neues Jahrbuch für Mineralogie, 1870, p. 753). Ehrenberg termed these bodies *morpholites*, and regarded them as inorganic in nature. Huxley (Journal Microscop. Science, 1868, VIII. No. 6) and Haeckel (Jenaische Zeitschrift, 1870, V. 3, p. 18) regarded them at first as portions of *Bathybius*, and designated them *coccoliths* (Fig. 1). The simple, disk-like varieties, convex on the upper side and concave on the lower, were termed *discoliths* (Fig. 1, *a*, *b*); while those composed of two closely applied disks of different sizes, resembling cuff-buttons in profile, were referred to as *cyatholiths* (Fig. 1, *c*). Coccoliths are only visible under powers of 800—1000 diameters, and exhibit, as a rule, a number of zones differing in their refractive indices, which are disposed about a single, double, or star-shaped central granule. Frequently large numbers of coccoliths become aggregated together in the form of freely suspended spherules or *coccospheres* (Fig. 2). Besides coccoliths, other minute, rod-shaped, calcareous bodies are sometimes met with, which are characterised by a discoidal or cruciform enlargement at one end. These are called *rhabdoliths* (Fig. 3), and their nodular aggregations *rhabdospheres*. Wyville Thomson, Carter, and Murray would identify coccospheres as unicellular algae, or as sporangia of algae, while Haeckel creates for them a special group, "*Calcocytae*," and assigns them provisionally to the Protophytes. According to Harting, however, the action of ammonia generated by the decomposition of albuminous matter held in solution in lime sulphate or lime chloride, causes the separation out of minute calcareous disks which bear a striking resemblance to coccoliths. Hence it would appear that the formation of excessively fine divided particles of lime in the sea should take place wherever there are decomposing albuminous, or nitrogenous substances present, and the calcium sulphate held in solution in the water becomes precipitated as calcium carbonate.



FIGS. 1—3.

FIG. 1, *a*, *b*.—*Coccoliths* (*Cyatholiths*) from the Atlantic Ocean; upper side and in profile (after Haeckel).

FIG. 1, *c*.—*Coccoliths* (*Discoliths*) from the Adriatic Sea; upper side and in profile (after O. Schmidt).

FIG. 2.—*Coccospheres* from the Atlantic Ocean (after Haeckel).

FIG. 3.—*Rhabdoliths* from the Adriatic Sea (after O. Schmidt). All figures magnified 700 diameters.

[1] Literature:

d'Orbigny, Alcide, Foraminifères fossiles du Bassin tertiaire de Vienne, 1846.

The test may be either unilocular, enclosing a single cavity (*Monothalamia*), or it may be divided by septa into a greater or lesser number of chambers (*Polythalamia*). Multilocular tests all grow from a single primordial chamber, which is either spheroidal or elliptical in contour, and augment rapidly by means of the successive apposition of new chambers, each a little larger than the first, and each being applied in turn against the general pseudopodial aperture of the preceding. All the chambers communicate with each other by means of pores through which the sarcode is protruded. According as the chambers are applied against one another in a linear series (*Stichostega*), in a spiral (*Helicostega*), in concentric rings (*Cyclostega*), in double or triple alternations of either straight (*Enallostega*) or spiral rows (*Entomostega*), or envelop one another in irregular coils disposed in from two to five different planes (*Agathistega*), a great variety of forms may be produced. These differences in external form, together with peculiarities in the mode of growth, were employed by Alcide d'Orbigny as a basis for the first detailed system of classification of the Foraminifera that has been devised. For specific diagnoses, the relative size and shape of the shell, and varieties of ornamentation, such as bands, lips, protuberances, points, spines, and the like, are of greatest significance.

In certain Foraminifera which secrete calcareous shells (*Nummulinidae*, *Miliolidae*, *Lagenidae*, *Orbulina*) a peculiar *dimorphism* has been observed, in that while some individuals have an extremely large primordial chamber (*megasphere*), others, although differing in nowise in external form and ornamentation, are characterised by an extremely minute primordial chamber (*microsphere*, Fig. 4). Those individuals which possess megaspheres are almost invariably much inferior in size to those having microspheres. De la Harpe refers this phenomenon to sexual differences; Munier-Chalmas and Schlumberger claim, on the other hand, that during the growth of those forms characterised by microspheres, the megaspheres, which are in all cases originally present, become absorbed and are replaced by an increased number of smaller chambers. Van den Broeck argues against these hypotheses, and attempts to explain dimorphism as the result of different modes of reproduction (fission and budding).

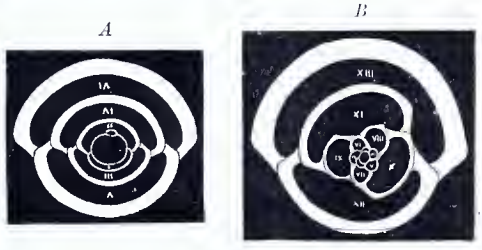


Fig. 4.

Biloculina Bradyi, Schlumb. Recent; Bay of Biscay. *A*, Small form with megasphere. *B*, Large form with microsphere. $^{15}/_{1}$ (after Schlumberger).

The finer structure of the shell or test, which has been thoroughly investigated by Carpenter and Williamson, is of great importance in the classification of the Foraminifera.

Chitinous tests are as a rule single-chambered (*monothalamous*), imperforate, and are provided with a single large-sized oral aperture. *Silicious*

Ehrenberg, C. G., Mikrogeologie, 1854, and Abhandlungen der Berliner Akademie, 1839.
Schultze, Max, Ueber den Organismus der Polythalamien, Leipzic, 1854.
Carpenter, W. B., Introduction to the Study of the Foraminifera, Ray Society, 1862.
Reuss, E. A., Numerous Reports in Sitzungsberichte der Wiener Akademie, from 1860 onwards.
Schwager, Conrad, Saggio di una Classificazione dei Foraminiferi, Bollet. Comitato Geol., 1876.
Brady, W. B., Monograph of Carboniferous and Permian Foraminifera, Palaeontograph. Soc., 1876.
Brady, W. B., Report on the Foraminifera, Scientific Results Challenger Exped., Zoology, XI., 1884.

tests consist of minute grains of sand, often intermingled with particles of lime and other foreign matter, the particles being held together by a siliceous or argillaceous cement. The tests are uniocular or multiocular, occasionally attain considerable size, and are either imperforate (Fig. 5, *A*), or, in addition to the either simple or sieve-like principal apertures, are punctured by

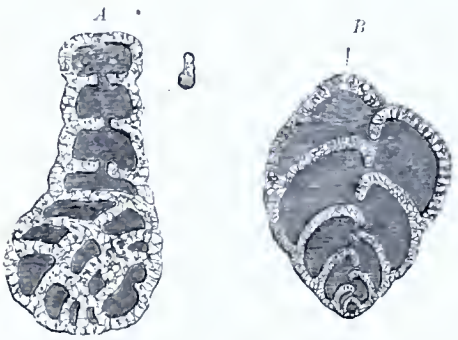


FIG. 5.

A, Section through an imperforate arenaceous test, highly magnified (*Haplophragmium irregulare*, Roem.) *B*, Section through a perforate arenaceous test showing coarse tubuli, highly magnified (*Plecanium gibbosum*, d'Orb.)

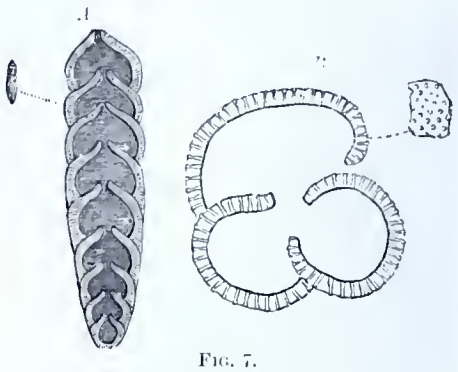


FIG. 7.

A, Section of vitreous perforate test with fine tubuli (*Nodosaria rapa*, d'Orb.) *B*, Portion of periphery, and section of a vitreous perforate test with coarse tubules less closely set together (*Globigerina conglomerata*, Schwager).

tubules, through which the pseudopodia are emitted (Fig. 5, *B*). Calcareous tests are also sometimes (*Miliolidae*, *Textularidae*) encrusted with agglutinated, compactly cemented sandy particles, and hence consist of an interior calcareous, and an exterior sandy-siliceous layer (Fig. 6). The greater number of

FIG. 6.

Climacammina textulariformis, Möller, sp. Perforate calcareous test invested with arenaceous envelope. $^{20}/_{1}$ (after Möller).

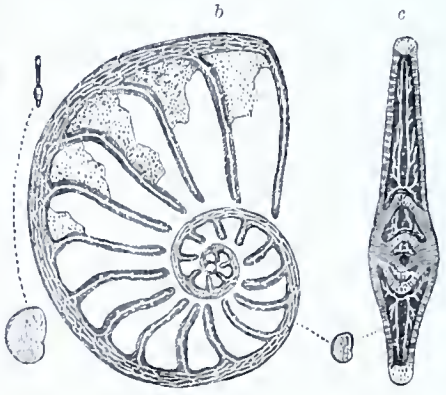


FIG. 8.

Operculina complanata, Bast. Miocene; Bordeaux. *a*, natural size; *b*, median longitudinal section; *c*, transverse section, greatly enlarged.

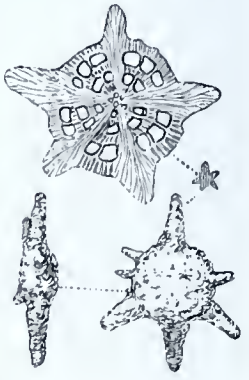


FIG. 9.

Calcarina calcitrapoides, Lam. Vitreous perforate test with spur-like supplemental skeleton traversed by canals.

Foraminifera, however, secrete tests composed of carbonate of lime, which may be either porcellaneous and imperforate, or vitreous and perforate in structure. In the first class (*Imperforata*) the shell is homogeneous, and appears in reflected light as an opaque mass (Fig. 4); in the second (*Perforata*) it is lustrous, transparent, and perforated by numerous fine tubules which pass through the walls radially. These tubules, which are visible on the peri-

phery as fine pores (foramina), are either all equal in diameter, being extremely small and closely set together (Fig. 7, *A*), or are larger in calibre and more widely separated from one another (Fig. 7, *B*). Certain vitreous, perforate Foraminifera are still further provided with coarser, anastomosing canals, which are restricted to definite parts of the shell, such as the septa, or the median plane of the spiral, in forms which are symmetrically convoluted. In the living state, these larger canals are occupied by bands or stolons of sarcode, but there is no connection between them and the other foramina or radial tubules. In many forms exhibiting more complicated structure, calcareous deposits are observed, which are distributed partly over the periphery, and partly in cavities and depressions within the shell itself. This is the so-called *intermediate* or *supplemental* skeleton, which often gives rise to peculiar excrescences on the periphery (Fig. 9), and in some cases is also pierced by tubules.

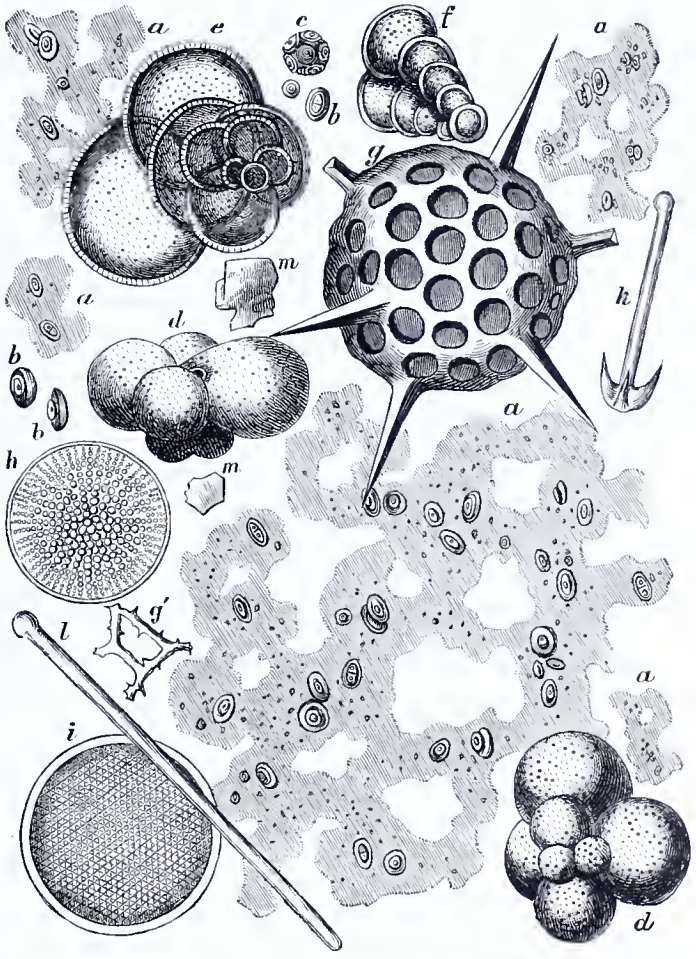


Fig. 10.

Deep-sea ooze magnified 700 diameters. *a*, *Bathybius* with Coccoliths; *b*, Individual Discoliths and Cyatholiths; *c*, Coccospheres; *d*, *Globigerina*; *e*, *Globigerina* with bursted test; *f*, *Textularia*; *g*, *g'*, *Radiolaria*; *h*, *i*, Diatoms; *k*, *l*, Sponge spicules; *m*, Mineral fragment.

Reproduction in the Foraminifera takes place either by means of fission, or by means of small nuclei which originate within the parent-individual, invest themselves with unilocular or multilocular tests, and forthwith abandon the parent shell, whereupon the latter falls to pieces.

The vast majority of Foraminifera are marine in habit. They occur in shallow water bordering the coasts, sometimes attached to algae, sometimes creeping on the bottom. A few genera are extraordinarily abundant in the open sea, occurring at different depths as free-swimming forms, and also on the floor of the ocean. Enormous quantities of their remains are spread over large tracts of the sea-bottom, and down to a depth of 2300 fathoms they remain an essential constituent of the chalk-like deep-sea ooze. This is a finely divided agglomeration of decomposed calcareous substances, such as the shells of

mollusks, corals, bryozoans, coccoliths, radiolarians, diatoms, sponges, and Foraminifera. Of the latter, certain genera are remarkable for their extraordinary abundance (*Globigerina*, *Orbulina*, *Pulvinulina*, *Biloculina*), (Fig. 10).

In the Atlantic and Pacific Oceans *Globigerina* ooze is the prevailing deep-sea deposit; in the North Sea, along the coast of Norway, *Biloculina* ooze. Numerous limestones and marls of older geological periods exhibit great similarity in structure and chemical composition to the now forming deep-sea oozes. White chalk (Fig. 11) is clearly a variety of abyssmal ooze, from which silicious constituents have become segregated out, and in which *Textularia* predominate instead of *Globigerina*. Certain of the Eocene limestones of the

Fig. 11.

Specimen of prepared white chalk from Meudon, as seen in transmitted light under power of 360 diameters, showing *Textularia*, *Globigerina*, and *Rotalia*.

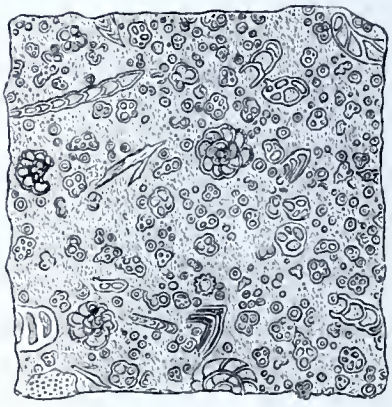


Fig. 12

Thin slice of Plänerkalk from Bohemia viewed in transmitted light under power of 50 diameters, showing sections of *Nodosaria*, *Rotalia*, *Frondicularia*, and numerous isolated *Globigerina* chambers.

Paris basin are composed almost exclusively of the tests of *Miliolidae*, while others are made up of *Alveolinae*, and *Nummulites*. During the Carboniferous period the chief rôle as rock-building organisms was played by *Fusilina*. Many dense, apparently homogeneous, or even semi-crystalline limestones of various ages, when examined microscopically in thin sections, are seen to be composed in large part of Foraminifera and other organic bodies (Fig. 12).

Fossil Foraminifera are best preserved, being usually detachable from the matrix, and at the same time occur most abundantly, in unconsolidated marls and clays which are interbedded with calcareous strata, or in limestones of a chalky or earthy character.

The tests of Foraminifera were first discovered by Janus Plancus, in 1730, on the beach of Rimini, and in the following year they were found by Beccari in the Pliocene of Bologna. They were long considered to be shells of mollusks, and were described by Breyn, Soldani, Fichtel, d'Orbigny, and others as *Cephalopoda foraminifera*, in distinction from *Cephalopoda siphonifera*. Dujardin, in 1835, was the first to recognise their true character as belonging to the Rhizopoda.

Foraminifera are divided into the four following sub-orders:—*Chitinosa*, *Agglutinantia*, *Porcellanea*, and *Vitro-Calcarea*.

Sub-order A. CHITINOSA. Schwager.

Test chitinous, imperforate, sometimes encrusted with agglutinated particles, and with pseudopodial aperture at one or at both extremities.

This group comprises the single family *Gromidae*, which is made up chiefly of fresh-water forms, and whose occurrence in a fossil state is unknown.

Sub-order B. AGGLUTINANTIA. Schwager.

Test composed of agglutinated sandy particles or other silicious foreign bodies, which are held together by a compact, silicious, or argillaceous cement.

Family 1. Astrorhizidae. Brady.

Test arenaceous, with rough exterior, usually unsymmetrical, often attaining considerable size; the sandy particles are sometimes only loosely cemented together; occasionally branching or developing radial prolongations; septa wanting.

Recent, and very abundant at great depths. Fossil in Palaeozoic and Jurassic formations.

Saccammina, Sars. (Fig. 13). Shell thick, with labyrinthiform interior; spherical, pear-shaped, or fusiform, with tubular prolongations at one or both ends; sometimes united together in chains. Ordovician (Ayrshire), Devonian (Canada), Carboniferous, and Recent. Entire strata of Carboniferous rock near Elfhills, Northumberland, are built up by *S. Carteri*, Brady.

Large-sized species of *Astrorhiza*, *Psammosphaera*, *Saccammina*, *Hyperammina*, and *Rhabdammina* are described by Häusler from the Upper Jurassic (Transversarius beds) of Switzerland.

Family 2. Lituolidae. Brady.

Test arenaceous or composed of agglutinated particles of various kinds; more or less regular in contour; divided by septa into a number of chambers, or more rarely single-chambered; free-swimming or attached; septal planes irregular, sometimes labyrinthic.

Recent species occur mostly at considerable depths.

Thurammina, Brady. Test free, monothalamous, irregularly spheroidal, usually with excrescences or spiny processes. Upper Jurassic and Recent.

Ammodiscus, Reuss. Test free, monothalamous, depressed, spirally coiled in a single plane, with terminal pseudopodial aperture. In all formations from Carboniferous to Recent.

Trochammina, Park. Jones (Fig. 16). Test thin, smooth, consisting of compact, ochre-like cement with embedded sandy particles; turbinate, or spirally wound like a snail-shell (trochoid); imperfectly chambered. Lias to Recent.

Placopsilina, d'Orb. (Fig. 15). Test rough, arenaceous, attached, and divided into pyriform or spherical chambers, which are joined in chains or are irregularly attached together. Lias to Recent.

Rheophax, Montf. (*Haplostiche*, Reuss), (Fig. 14). Test free, rod-shaped or slightly bent; septa simple (*Rheophax*) or labyrinthic (*Haplostiche*); pseudopodial aperture at extremity. Carboniferous to Recent.

Lituola, Lam. (*Haplophragmium*, Reuss), (Fig. 17). Test free, crosier-shaped or spirally wound. General aperture simple or sieve-like; septa simple (*Haplophragmium*) or labyrinthic (*Lituola*). Carboniferous to Recent; particularly abundant in Jurassic and Cretaceous.

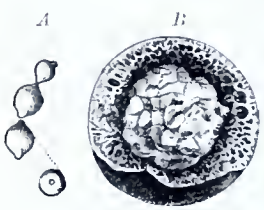


Fig. 13.

A, *Saccammina Carteri*, Brady. Carboniferous Limestone; Elfhills, Northumberland. $^1/_1$. *B*, Fractured test, filled with interior calcite. $^{10}/_1$ (after Brady).

Fig. 14.

Haplostiche horrida, Schwager. Upper Jurassic (Impressa clay); Gruibingen, Württemberg.

Fig. 15.

Placopsilina rostrata, Quenst. sp. Upper Jurassic (Impressa clay); Reichenbach, Württemberg.

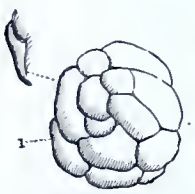


Fig. 16.

Trochammina proteus, Karrer. Vienna sandstone (Senonian); Hütteldorf, near Vienna.

Fig. 17.

Lituola (*Haplophragmium*) *irregulare*, Roemer. Scaphiten-Pläner; Kröndorf, Bohemia.

Family 3. **Orbitolinidae.** Zittel.

Test silicious, imperforate, bowl-shaped, and composed of concentric rings which are partitioned off into numerous chambers.

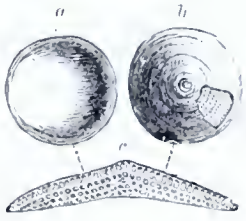


Fig. 18.

Orbitolina concava, Lam. Cenomanian; Urschelau, Bavarian Alps. *a*, Inferior surface; *b*, Superior surface; *c*, Transverse section (enlarged).

Orbitolina, Lam. (Fig 18). Test silicious, with agglutinated sandy particles; bowl-shaped to depressed conical; upper side convex, lower side slightly hollow. Periphery smooth, or with concentric bands, imperforate. Test composed of multilocular rings, the chambers communicating with one another on all sides by means of pores. The peripheral portion of each chamber is divided up into smaller compartments by two secondary septa disposed at right angles to each other. Very abundant in the Lower (*O. lenticularis*, Lam.) and Upper Cretaceous (*O. concava*, Lam.)

Sub-order C. PORCELLANEA. Schwager.

Test calcareous, porcellaneous, imperforate.

Under starved conditions (*e.g.* in brackish water) the test may assume a chitinous or arenaceous character, or may become encrusted with a thin, homogeneous, silicious envelope. The majority of recent forms inhabit shallow water; only a few occur at abyssmal depths.

Family 1. **Nubeculariidae.** Brady.

Test comparatively large-sized, usually attached, extremely irregular in contour, with one or with several general apertures. Triassic to Recent.

The recent genus *Nubecularia*, Dfr., belonging to this family occurs fossil in all formations from the Triassic onward, and is particularly abundant in the Miocene (Sarmatian stage) of Bessarabia, Russia.

Family 2. **Peneroplidae.** Schwager.

Test plano-spiral or cyclical, bilaterally symmetrical, usually polythalamous, more rarely monothalamous. Triassic to Recent.

Cornuspira, Schultze (Fig. 19). Test composed of numerous plano-spiral convolutions; oral aperture simple, terminal; monothalamous. Lias to Recent.

Peneroplis, Montf. (Fig. 20). Test discoidal, complanate, polythalamous; direction of growth primarily spiral, gradually becoming rectilinear, while

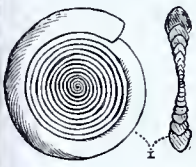


Fig. 19

Cornuspira polygyra, Reuss. Oligocene; Hungary.

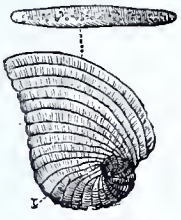


Fig. 20.

Peneroplis planatus, Montfort. Recent; Mediterranean.

Fig. 21.

Orbiculina nummis malis, d'Orb. Pliocene; Sienna, Italy.

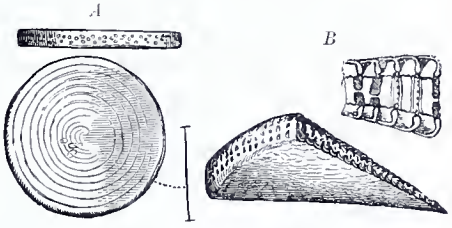


Fig. 22.

A, *Orbitolites complanata*, Lam. Eocene (Calcaire Grossier); Paris. *B*, Portion of same enlarged.

rapidly increasing in breadth. Septa perforated by numerous foramina. Tertiary to Recent.

Orbiculina, Lam. (Fig. 21). Test discoidal; segments spiral at commencement, later becoming annular; polythalamous, septation regular, chambers subdivided; septa and walls of segments perforate. Tertiary to Recent.

Orbitolites, Lam. (Fig. 22). Test discoidal, circular in contour, both sides slightly concave in the centre, of comparatively large dimensions, and composed of segments which are disposed concentrically about a few spirally wound primordial chambers. Polythalamous; septa radially disposed, and perforated by symmetrically distributed foramina. In the more complicated forms the principal segments are covered over on both sides by a thin, superficial, multilocular layer, the chambers of which are likewise arranged in concentric rings, and communicate with the principal chambers by means of pores. Lias (*O. praecursor* and *O. circumvulva*, Gümb.), Cretaceous (*O. macropora*,

Fig. 23.

Alveolina Boscі, d'Orb. Eocene (Calcaire Grossier); Paris. *A*, Frontal aspect. *B*, Test laid open so as to show conformation of interior; considerably enlarged.

d'Orb.), Tertiary (*O. complanata*, Lam.), and Recent. An important rock-building genus.

Alveolina, Bosc. (*Borelis*, Montf.), (Fig. 23). Test fusiform, elliptical, or spherical, usually elongated in the axis of convolution, and composed of spirally wound segments which completely envelop one another. Each segment is partitioned off into long, narrow chambers by septa arranged at right angles to the axis, and these are subdivided into chamberlets by a second set of septa running transversely to the first set. Each of the secondary chamberlets communicates with the adjacent primary chamber by means of a single round aperture. In certain recent species the secondary chamberlets are also subdivided. The genus begins in the Cenomanian, continues in extraordinary profusion, and becomes a most important rock-builder in the Eocene (Calcaire Grossier of the Paris basin, Alveolina limestone of Istria, Dalmatia, Greece, and the Libyan Desert).

Family 3. **Miliolidae.** Carpenter.

Test either entirely composed of coil-like segments, or convoluted only at commencement. Primordial chamber dimorphous. Triassic to Recent.

Miliola, Lam. (Figs. 24, 25). Segments disposed in coil-shaped loops about a few spirally wound primordial chambers. Each loop is constricted at

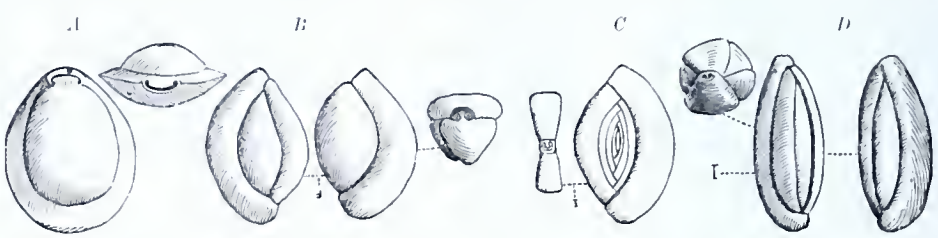


Fig. 24.

A, *Biloculina inornata*, d'Orb. From the Miocene Tegel; Baden, near Vienna. *B*, *Triloculina gibba*, d'Orb. Oligocene sand from Astrupp. *C*, *Spiroloculina Badensii*, d'Orb. Miocene Tegel; Baden, near Vienna. *D*, *Quinqueloculina saxorum*, d'Orb. Eocene (Calcaire Grossier); Grignon, near Paris.

the extremities so as to form a septum of its own walls. Terminal pseudopodial aperture either curving in the form of a crescent about a tooth-like projection, or branching dendritically (*Lacazina*). Forms having all the segments disposed in a single plane, and all externally visible, are grouped together in the sub-genus *Spiroloculina*, d'Orb.; with all the segments completely enveloping one another, *Biloculina*, d'Orb.; segments disposed in three or in five different planes, *Triloculina* and *Quinqueloculina*, d'Orb. The great variety and extraordinary profusion of this genus combine to make it one of the most important of the rock-building Foraminifera. Massive beds of Eocene limestone (Paris basin, Pyrenees) are

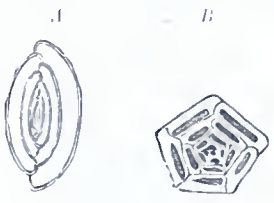


Fig. 25.

A, Longitudinal section of *Biloculina inornata*, d'Orb. (enlarged). *B*, Transverse section of *Quinqueloculina saxorum*, d'Orb. (enlarged).

Fig. 26.

Fabularia discolithes, Defr. Eocene (Calcaire Grossier); Paris.

Fig. 27.

Vertebralina mucronata, d'Orb. Recent; Mediterranean.

made up of Miliola remains; at the present day calcareous deposits are being formed by Biloculina in the North Sea west of the coast of Norway. Miliola begins in the Triassic, and attains its maximum development in the Tertiary and Recent periods.

Fabularia, Defr. (Fig. 26). Like *Biloculina*, but relatively larger. Oral aperture sieve-like; chambers not hollow, but filled with porcellaneous calcareous matter, and perforated by numerous anastomosing canals which run parallel with the axis of convolution. Abundant in Eocene of the Paris basin.

Vertebralina, d'Orb. (Fig. 27). Test consisting of coil-shaped loops at commencement, afterwards becoming rectilinear. Tertiary and Recent.

Sub-Order D. VITRO-CALCAREA. Schwager.

Test calcareous, vitreous, perforate; more rarely silicious, or silicious with vitro-perforate substratum; punctured by numerous fine tubules for the emission of pseudopodia. Silurian to Recent.

Family 1. Lagenidae. Carpenter.

Test perforated only by very fine and closely-set tubules, without supplemental skeleton or canal system.

Lagena, Walker (Fig. 28, *A*). Test single-chambered, spherical, ovate, or flask-shaped, with terminal oral aperture. Silurian to Recent.

Nodosaria, Lam. (Fig. 28, *B*). Test rod-shaped: chambers arranged in a

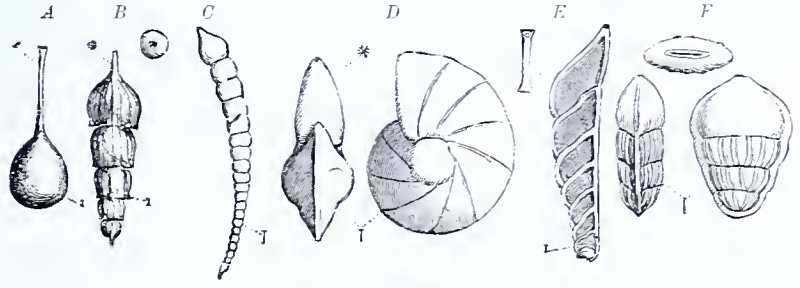


FIG. 28.

A, *Lagena semistriata*, Williamson. Antwerp Crag (Pliocene); Antwerp. *B*, *Nodosaria spinicosta*, d'Orb. Tegel (Miocene); Baden, near Vienna. *C*, *Dentalina elegans*, d'Orb. Same locality. *D*, *Cristellaria rotulata*, Lam. Scaphiten-Pläner (Turonian); Bohemia. *E*, *Vaginulina recta*, Reuss. Neocomian; Salzgitter, Hanover. *F*, *Lingulina costata*, d'Orb. Tegel (Miocene); Baden, near Vienna.

straight line and set off from one another by constrictions; oral aperture round, terminal. Widely diffused from Silurian to Recent.

Dentalina, d'Orb. (Fig. 28, *C*). Like the preceding, but slightly bent. Carboniferous to Recent.

Vaginulina, d'Orb. (Fig. 28, *E*). Test straight, laterally compressed; segments flattened, with obliquely directed septa. Triassic to Recent.

Marginulina, d'Orb. Early segments curved or helicoid, later ones rectilinear. Oral aperture slit-like. Triassic to Recent.

Cristellaria, Lam. (Fig. 28, *D*). Test regularly plano-spiral, with convolutions completely enveloping one another. Oral aperture round. Triassic to Recent.

Lingulina, d'Orb. (Fig. 28, *F*). Test straight, compressed; segments attached in rectilinear series. General aperture terminal, slit-like. Triassic to Recent.

Glandulina, d'Orb. (Fig. 29, *A*). Test short, ovate; segments united in rectilinear series, half-embracing one another. General aperture round, terminal, usually tubulated. Triassic to Recent.

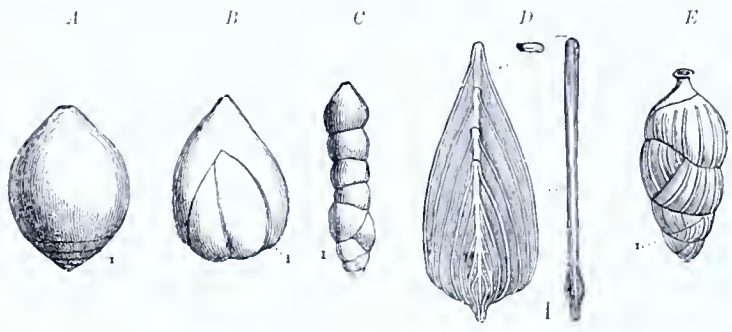


Fig. 29.

A, *Glandulina inflata*, Bornem. Septarienthon (Oligocene); Hermsdorf. *B*, *Polymorphina inflata*, Williamson. Recent; German Ocean. *C*, *Dimorphina sp.* Pliocene; Sienna, Italy. *D*, *Frondicularia Goldfussi*, Reuss. Scaphiten-Pläner; Dülmen, Westphalia. *E*, *Uvigerina pygmaea*, d'Orb. Tegel (Miocene); Baden, near Vienna.

Frondicularia, Defr. (Fig. 29, *D*). Test straight, extremely compressed, and foliately expanded. Chambers greatly reflexed, laterally embracing one another. General aperture round, terminal. Triassic to Recent.

Polymorphina, d'Orb. (Fig. 29, *B*). Segments irregularly helicoid, or arranged in double series more or less enveloping each other and varying in shape. General aperture round, terminal. Triassic to Recent.

Dimorphina, d'Orb. (Fig. 29, *C*). Early chambers irregularly or triserially disposed, later ones following in a straight line. Cretaceous to Recent.

Uvigerina, d'Orb. (Fig. 29, *E*). Segments dissimilar, disposed in triple series, and spirally wound like a snail-shell. Eocene to Recent.

Family 2. **Textularidae.** Schultze.

Test in larger forms arenaceous, with calcareous basis perforated by coarse tubules; in smaller forms vitreous, perforate; segments regularly or only in part arranged in two (rarely more than two) alternating series.

Textularia, Defr. (Fig. 30, *A*). Test usually elongated, straight, tapering, or turbinated. Chambers biserial, alternating, and communicating with each other by means of slit-like apertures. Carboniferous to Recent. Extremely abundant in the White Chalk.

The genera *Textularia*, s. str., *Grammostomum* (Fig. 30, *D*), and *Bolivina* (Fig. 30, *B*) of the calcareous forms; and *Plecanium* (Fig. 30, *C*), *Bigenerina*, *Gaudryina* (Fig. 30, *E*), *Clavulina* (Fig. 30, *F*), and *Verneuilina* are founded upon various minor modifications.

Bulimina, d'Orb. (Fig. 31, *A*, *B*). Test calcareous, the alternating chambers arranged in an elongated spire. Triassic to Recent.

Valvulina, d'Orb. (Fig. 31, *E*). Test arenaceous with calcareous basis. Chambers in triple series arranged in screw-like spiral. Carboniferous to Recent.

Climacammina, Brady (*Cribrostomum*, Möller), (Fig. 31, *B*, *C*). Test arenaceous with calcareous basis. Chambers biserial, rectilinear. Oral aperture porous. Abundant in Carboniferous Limestone. (cf. *Bigenerina*, d'Orb.)

Tetrataxis, Ehrbg. (Fig. 31, *F*). Test calcareous, conical. Alternating chambers arranged in a turbinate spire. Carboniferous Limestone.

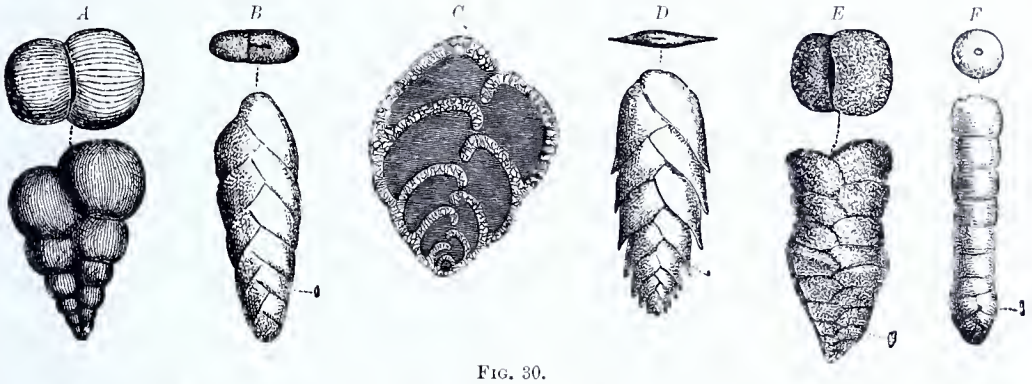


FIG. 30.

A, *Textularia globifera*, Reuss. Upper Cretaceous (Senonian); Pattenauer Stollen, near Traunstein, Bavaria. *B*, *Bolivina incrassata*, Reuss. Upper Cretaceous; Götzreuther Graben, near Siegsdorf, Bavaria. *C*, *Plecanium gibbosum*, d'Orb. Pliocene; Sienna, Italy. *D*, *Grammostomum* (*Vulvulina*) *gramen*, d'Orb. Recent; Cuba. *E*, *Gaudryina rugosa*, d'Orb. Upper Cretaceous; Götzreuther Graben, near Siegsdorf. *F*, *Clavulina communis*, d'Orb. Miocene; Baden, near Vienna.

Cassidulina, d'Orb. (*Ehrenbergina*, Reuss) (Fig. 31, *G*). Test calcareous, the

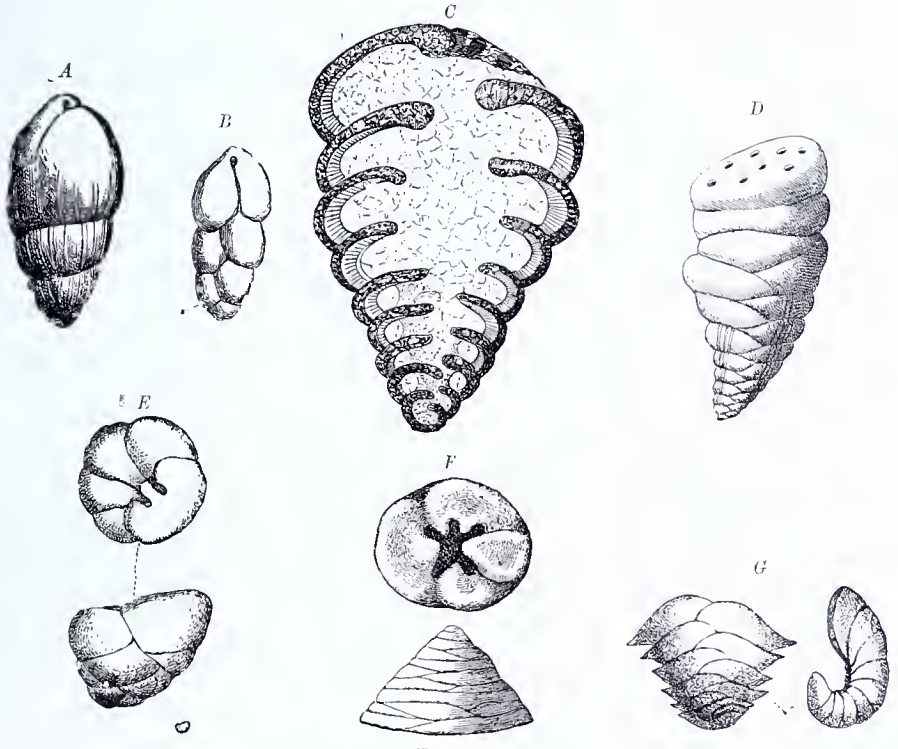


FIG. 31.

A, *Bulimina Buchiana*, d'Orb. Miocene (Leithakalk); Nussdorf, near Vienna. *B*, *Bulimina pupoides*, d'Orb. Same locality. *C*, *Climacammina textulariformis*, Möller. Carboniferous Limestone; Dugno, Russia. Longitudinal section. $^{20}/_{1}$ (after Möller). *D*, *Climacammina pyriforme*, Möller, sp. Carboniferous Limestone; Sloboda, Russia. $^{20}/_{1}$ (after Möller). *E*, *Valvulina sp.* Eocene (Calcaire Grossier); Grignon, near Paris. *F*, *Tetrataxis conica*, Ehrbg. Carboniferous Limestone; Bachtin, Russia. $^{20}/_{1}$ (after Möller). *G*, *Ehrenbergina serrata*, Reuss. Miocene; Baden, near Vienna.

alternating biserial segments either completely or only partially coiled. Tertiary and Recent.

Family 3. **Globigerinidae.** Carpenter.

Test free, calcareous, perforated by coarse tubules; monothalamous or polythalamous; chambers globular, either irregularly disposed or imperfectly spiral.

Of the two most important genera belonging to this family, *Orbulina*, d'Orb. (Fig. 32, *A*), is uniloeular, and *Globigerina*, d'Orb. (Fig. 32, *C*), multiloeular. The individual chambers usually conduct into a common central canal. In both genera the test is often covered with extremely delicate calcareous spines, which, however, are very easily broken off, and are never preserved in the fossil state. These genera are excessively diffuse in modern deep-sea deposits (Globigerina ooze); they occur sparingly in Mesozoic formations, beginning with the Triassic, and first rise to importance during the late Tertiary period.

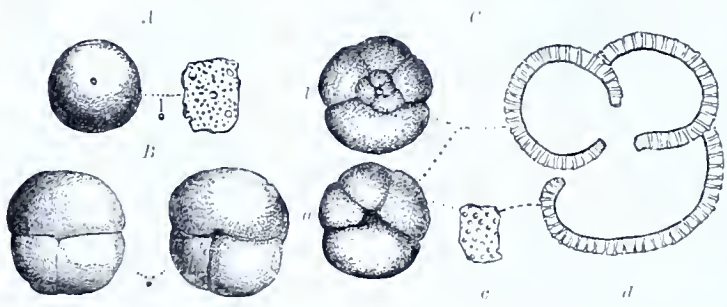


Fig. 32.

A, *Orbulina universa*, Lam. Pliocene; Sienna, Italy. *B*, *Sphaeroidina Austriaca*, d'Orb. Miocene Tegel; Baden, near Vienna. *C*, *Globigerina conglomerata*, Schwager. Pliocene; Kar Nikobar Island. *a*, Inferior surface; *b*, Superior surface; *c*, Portion of periphery; *d*, Transverse section enlarged.

Sphaeroidina, d'Orb. (Fig. 32, *B*). Cretaceous to Recent.

Family 4. **Rotalidae.** Carpenter.

Test calcareous, rarely arenaceous or silicious, finely or coarsely perforated, frequently with intermediate skeleton, free or attached, turbinate or discoidal in contour. Segments usually arranged in an elongated spire, although in some forms irregularly disposed.

Discorbina, Park. Jones (Fig. 33, *A*, *B*). Test coarsely perforated, turbinoid. Inferior surface broad and flat; umbilicus often filled with deposit of intermediate skeleton. Cretaceous to Recent.

Planorbulina, Park. Jones (Fig. 33, *C*). Test coarsely perforated, complanate, usually attached, superior and inferior surfaces dissimilar; early segments arranged in depressed spire, subsequently becoming cyclical. Lias to Recent. The d'Orbignyan sub-genera *Truncatulina*, *Anomalina*, *Planulina*, etc., are based upon different modifications in form.

Rotalia, Lam. (Fig. 34, *A*). Test finely perforated, with segments in turbinoid spire. Septa composed of two slightly separated lamellae, with anastomosing canals occupying the intermediate space. Basis often thickened by supplemental skeleton. (?) Silurian. Upper Jurassic to Recent.

Pulvinulina, Park. Jones (Fig. 34, *B*). Rotaliform, but septa single and without interseptal canal-system. Lower Lias to Recent.

Endothyra, Phill. (Fig. 34, *C*). Test calcareous; composed of an exterior coarsely perforated, and an interior compact layer consisting of minute grains of limey matter; polythalamous; irregularly spiral. General aperture

porous. Abundant in Carboniferous Limestone, and according to Brady, also recent.

Calcarina, d'Orb. (Fig. 35). Test discoidal, with dissimilar upper and

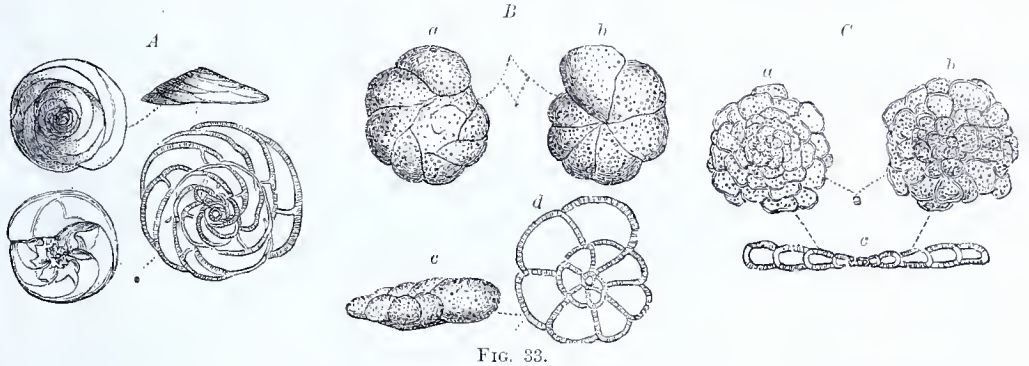


FIG. 33.

A, *Discorbina* (*Asterigerina*) *planorbis*, d'Orb. Miocene (Leithakalk); Nussdorf, near Vienna. *B*, *Discorbina sp.* Recent. *a*, Under side; *b*, Upper side; *c*, Lateral view; *d*, Median section. *C*, *Planorbulina Mediterranensis*, d'Orb. Recent; Mediterranean. *a*, Inferior surface; *b*, Superior surface; *c*, Transverse section.

lower surfaces, chambers spirally wound. Exterior encrusted with supplemental skeleton, which fills up all depressions, and builds spiny or spur-like

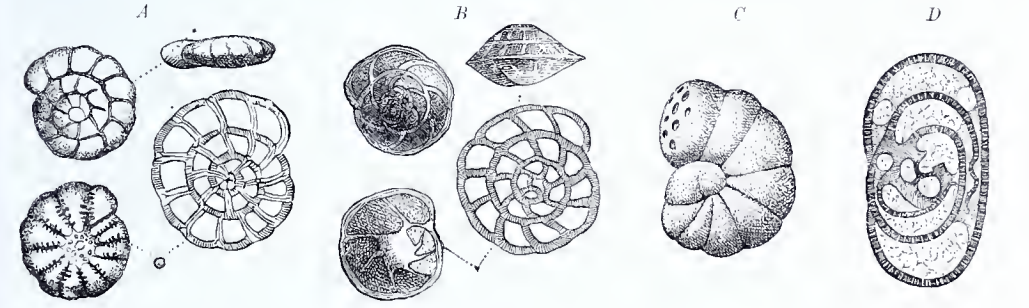


FIG. 34.

A, *Rotalia Beccari*, Lin. Pliocene; Sienna, Italy. *B*, *Pulvinulina Partschi*, d'Orb. Miocene (Tegel); Baden, near Vienna. *C*, *Endothyra Panderi*, Möller. Carboniferous Limestone; Russia. $^{20}/_{1}$. *D*, *Endothyra parva*, Möller. Carboniferous Limestone; Russia. Longitudinal section. $^{100}/_{1}$.

appendages traversed by coarse canals. Upper Cretaceous to Recent. Particularly abundant in Maestricht Chalk.

Tinoporus, Montf. *Patellina*, Williamson.

The recent genera *Carpenteria*, Gray, *Polytrema*, Gray, *Rupertia*, Jones, etc., are distinguished by their extremely irregular, usually attached, coarsely perforated tests, which occasionally attain considerable size, and often contain agglutinated, sandy, or other foreign particles. *Thalamopora*, Roem., occurring in the Cretaceous, probably also belongs to this family.

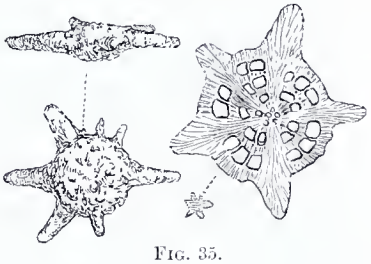


FIG. 35.

Calcarina calcitrapoides, Lam. Upper Cretaceous (Tuffkreide); Maestricht, Holland.

Family 5. **Fusulinidae.** Möller.

Test calcareous, perforate, polythalamous, fusiform or spherical, composed of numerous spirally inrolled whorls (symmetrically involute). The whorls are divided

into principal chambers by vertically directed septa, and these are further broken up into secondary chamberlets by transverse partitions. Septa single or more rarely double.

Schwagerina, Möll. Test spherical, finely perforated. Primary and secondary septa simple, thin, straight; secondary chamberlets communicating with the next following principal chamber by means of a basal aperture.

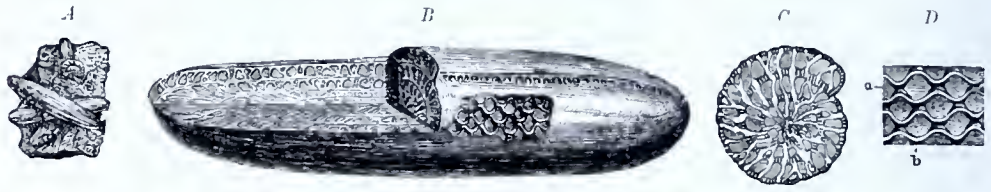


FIG. 36.

A, *Fusulina cylindrica*, Fisch. Carboniferous Limestone; Saranisk, Russia. Natural size. *B*, *C*, Same species showing various cross-sections enlarged. *D*, Enlarged section showing chambers communicating by means of foramina (*a*, *b*).

Abundant in Carboniferous Limestone of Japan, China, Sumatra, North America, and Russia.

Fusulina, Fischer (Fig. 36). Test fusiform, laterally elongated like *Alveolina*, coarsely perforated. Septa of principal chambers undulating, and united so as to form secondary chamberlets. Excessively abundant in Carboniferous Limestone of Europe (Russia), Asia, and North America.

Family 6. **Nummulinidae.** Carpenter.

Test calcareous, finely perforated, lenticular or discoidal, often attaining considerable dimensions; polythalamous, and composed either of discoidal spiral whorls or of cycloidal rings. Pillars of compact intermediate skeleton present, and in most forms also an anastomosing canal-system occupying interseptal spaces and certain other portions of the shell.

Archaediscus, Brady. Test lenticular, unsymmetrical, spirally coiled. The segments irregularly constricted and expanded so as to form chambers. Septa and canal-system wanting. Carboniferous Limestone.

Amphistegina, d'Orb. (Fig. 37). Test lenticular, slightly inequilateral, spirally rolled. Whorls divided into chambers by numerous single septa in which canals are not present; solid wedge-shaped deposit of intermediate skeleton near the umbilicus. On one side the volutions completely enclose one another as far as the centre, on the other they overlap only partially by means of alar prolongations extending inwards. Chambers communicate with each other by means of a slit along the basis. Miocene to Recent. Particularly abundant in Miocene.

Operculina, d'Orb. (Fig. 38). Test discoidal, complanate, composed of three to six rapidly expanding spiral whorls, which are polythalamous and non-involute. Septa and marginal cord traversed by a direct canal-system, which gives off numerous branches. Cretaceous to Recent. Particularly abundant in Eocene.

Heterostegina, d'Orb. (Fig. 39). Like *Operculina*, but with chambers subdivided by secondary septa into chamberlets. Tertiary and Recent.

Nummulites, d'Orb. (*Phacites*, Gesner; *Lenticulites*, Lam.), (Figs. 40-42). Test

symmetrically lenticular or discoidal, composed of numerous spirally arranged polythalamous volutions, and usually with columnar intermediate skeleton, which forms small excrescences on the periphery. The septa and marginal

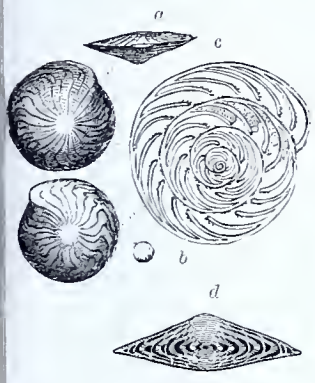


FIG. 37.

Amphistegina Haueri, d'Orb. Miocene (Leithakalk); Nussdorf, near Vienna. *a*, Exterior views, enlarged; *b*, Natural size; *c*, Median section, greatly enlarged; *d*, Transverse section, greatly enlarged.

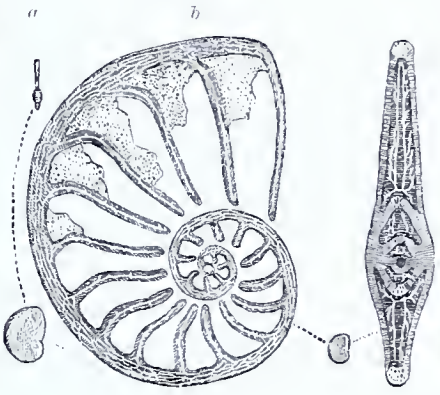


FIG. 38.

Operculina complanata, Bast., sp. Miocene; Bordeaux. *a*, Natural size; *b*, *c*, Median and longitudinal sections, greatly enlarged.

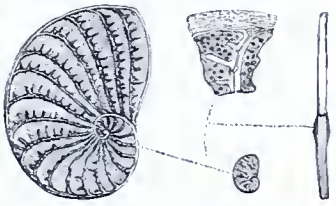


FIG. 39.

Heterostegina costata, d'Orb. Miocene (Leithakalk); Nussdorf, near Vienna.

cord contain a coarse, anastomosing canal-system, as in *Operculina*. Primordial chamber spherical, sometimes large, sometimes exceedingly minute in size. The whorls either merely embrace one another (*Assilina*) (Fig. 41), or they completely envelop one another by means of alar prolongations reaching

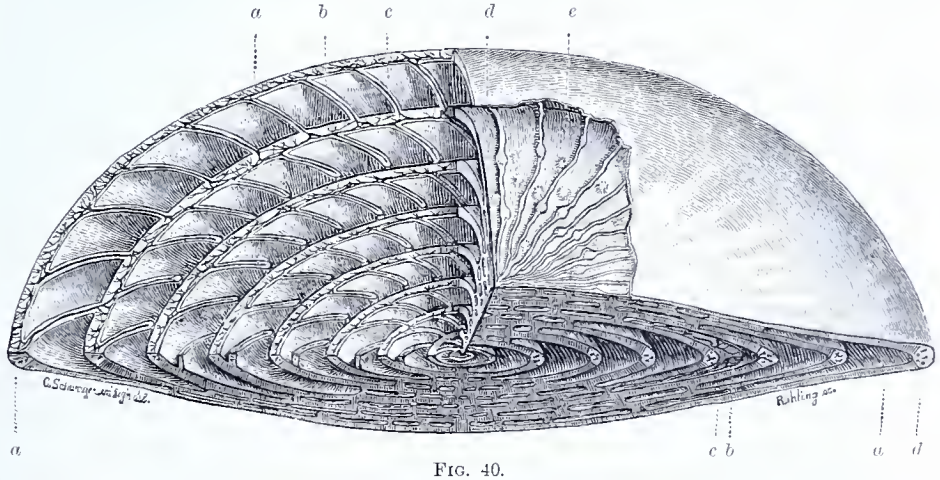


FIG. 40.

Nummulites cfr. Lucasanus, Dfr. Eocene; Kressenberg, Upper Bavaria. Several times enlarged. *a*, Marginal cord with canal-system; *b*, Septal plane with interseptal canal-system; *c*, Interior of chamber; *d*, Finely perforate periphery; *e*, Small pillars of intermediate skeleton.

inwards to the centre (*Nummulina*). The septa are pierced in the median plane by an oblique slit-like aperture, and also extend into the saddle-shaped alar prolongations of the chambers. They are directed in the groups *Radiatae* and *Striatae* in straight or slightly curved lines (Figs. 40 and 42, *C*); in the *Sinuatae* they follow meandering courses (Fig. 42, *A*); and in the *Reticulatae* (Fig. 42, *B*) they form an interlacing network by means of connecting pro-

cesses. The ramifications of these lateral processes (*Filet cloisonnaire*) may be readily seen on fracturing a portion of the test, and are a valuable aid in the determination of species. The oldest Nummulites (*N. pristinus*, Brady) occur very sparsely in the Carboniferous Limestone and Upper Jurassic, but are distinguished from the typical later forms by the absence of an interior canal-system in the marginal cord. The typical Nummulites which are so characteristic of the Eocene (Nummulitic limestone) in Europe, North Africa, Asia, and Central America, often build up massive formations. The largest species (*N. Gizehensis*, Ehrbg., *N. orbiculatus*, Schafh.) attain a diameter of 60 mm.; the smallest species does not exceed 2 mm.; recent representatives comparatively scarce.

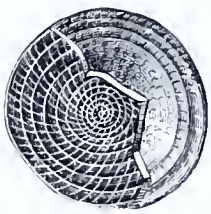


Fig. 41.

Nummulites (*Assilina*) *exponens*, Sow. Eocene; Pyrenees.

Polystomella, d'Orb. (Fig. 44); *Nonionina*, d'Orb.; *Cycloclypeus*, Carp. Tertiary and Recent.

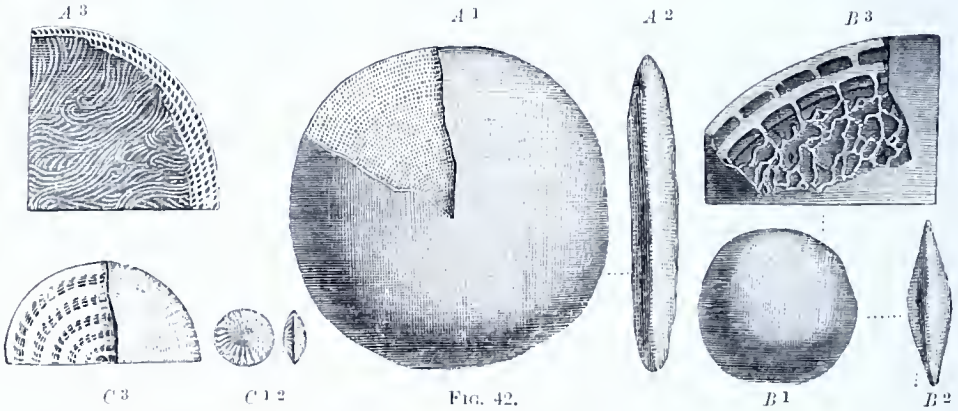


Fig. 42.

A, *Nummulites Gizehensis*, Ehrbg. Eocene; Libyan Desert. Natural size. *A* 3, Specimen with eroded peripheral portion, showing arrangement of septa. *B* 1 2, *Nummulites laevigatus*, Lam. Calcaire Grossier; Paris. Natural size. *B* 3, Portion of same enlarged. *C* 1 2, *Nummulites Ramondi*, Defr. Eocene (Nummulitic limestone); Pyrenees. Natural size. *C* 3, Enlarged section.

Orbitoides, d'Orb. (*Hymenocyclus*, Bronn; *Lycophrys*, Montf.), (Fig. 45). Test discoidal, with circular or stellate contour, often bent, exterior smooth or with

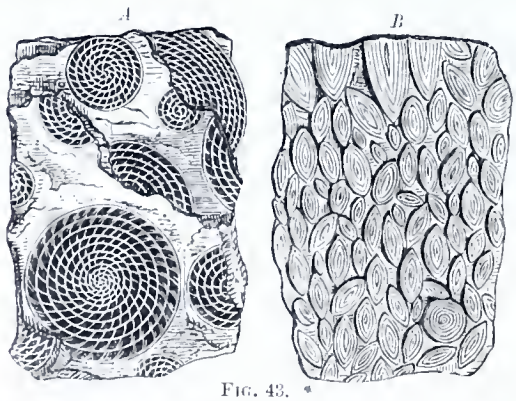


Fig. 43.

A, Nummulitic limestone with horizontal sections of *N. distans*, Pusch. Peyrehorade, in the Pyrenees. *B*, Nummulitic limestone showing sections of *N. Lucasanus*, Defr. Zakophane in the Carpathians.

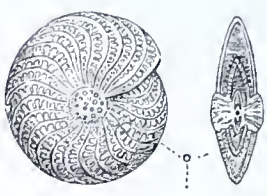


Fig. 44.

Polystomella crispa, Lam. Pliocene; Sienna, Italy. (Highly magnified.)

radial striae, and composed of numerous concentric annuli disposed about a

primordial spiral of three to five whorls. The rings are divided by transverse partitions into small rectangular chambers, and the septa and marginal cord are traversed by canals. Superimposed over the median series of principal chambers on both sides are several layers of flattened secondary chamberlets,

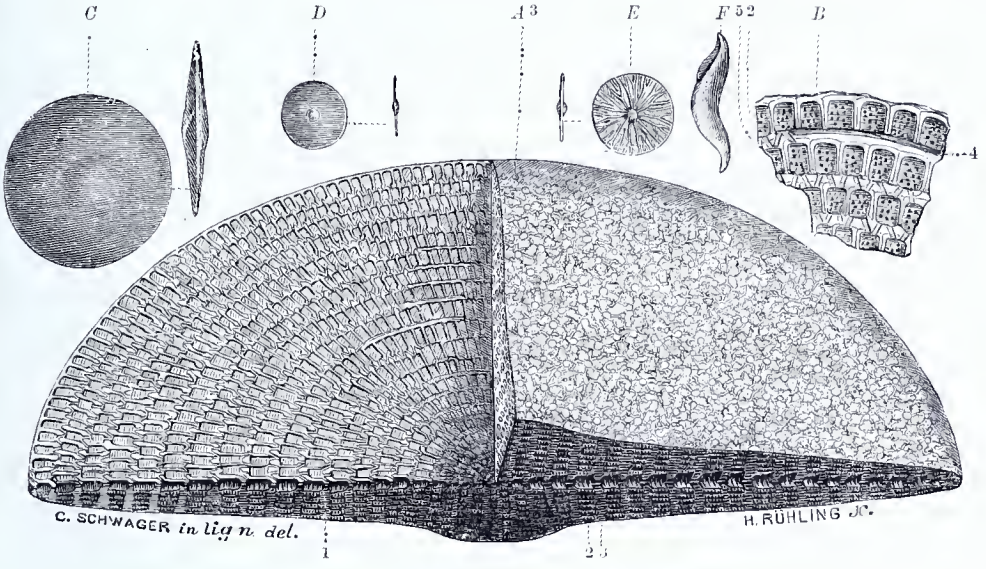


FIG. 45.

A, Orbitoides papyracea, Boubée. Eocene (Ferruginous sandstone); Kressenberg, Upper Bavaria. (Greatly enlarged). [1] Median chambers; [2] Lateral chambers; [3] Compact pillars of intermediate skeleton. *B*, Portion of median transverse section, highly magnified; [2] Lateral chambers with perforate walls; [4] Canal-system of cyclical marginal cord; [5] Tubules connecting adjacent chambers. *C*, Periphery and profile of same, natural size. *D, Orbitoides tenella*, Gümbel. Eocene; Kressenberg. (Natural size.) *E, Orbitoides varicostata*, Gümbel. Eocene; San Martino, near Verona. (Natural size.) *F, Orbitoides ephippium*, Sow. Eocene; Kressenberg. (Natural size.)

which are likewise disposed in concentric rings. Very abundant in the Eocene, associated with *Nummulites;* rare in Upper Cretaceous and Miocene.

Dawson, Carpenter, and various other authors have referred the so-called *Eozoon* occurring in crystalline limestone of the Archaean (Laurentian) period to the Foraminifera; but the elaborate investigations of Möbius have shown that neither *Eozoon* nor *Archaeosphaerina* can be regarded as organic structures, but are mineral segregations.

Range and Distribution of Fossil Foraminifera.

Of the over 2000 species of Foraminifera that have been described, about two-thirds are known in a fossil state. The longevity of certain genera and species is remarkable, many of them persisting, according to Parker, Jones, Brady, and others, throughout a number of formations of various ages.

The earliest forms occur very sparingly in the Silurian of St. Petersburg, Siberia, and Scotland. They are for the most part poorly preserved, those from Petersburg being recognisable only as glauconitic casts, belonging in part to silicious shell-bearing genera (*Placopsilina*, *Saccamina*), and in part to vitreo-perforate genera (*Nodosaria*, *Lagena*, *Globigerina*, *Rotalia*). The Devonian is also very poor in Foraminifera remains; but, on the other hand, the Carboniferous yields an abundant and considerably varied fauna; in fact, certain genera (*Fusilina*, *Schwagerina*, *Saccamina*, *Endothyra*) build up limestone de-

posits occasionally of great thickness. Numerous representatives of the *Lagenidae* (*Nodosaria*, *Dentalina*, etc.), *Textularidae*, *Rotalidae*, and even the *Nummulinidae* accompany the rock-building forms, and continue for the most part throughout the Permian. Except in the Alps, the Triassic is almost destitute of Foraminifera, and even the pure limestones and dolomites of the Alpine Triassic have usually become so altered by metamorphism as to render the recognition of tests well-nigh impossible. Notwithstanding, Globigerina limestone has been discovered in the Upper Triassic of the Northern Alps, and tests of *Cristellaria*, *Marginulina*, *Globigerina*, *Textularia*, *Biloculina*, etc., are found in the St. Cassian beds.

Certain argillaceous and calcareous strata of the Lias and Jura contain vast quantities of minute, vitreo-perforate or silicious Foraminifera. In the Cretaceous, *Textularia*, *Rotalia*, *Cristellaria*, *Globigerina*, *Miliola*, and *Coccoliths* are essential constituents of the White Chalk. Individual beds of the Maestricht Chalk consist almost entirely of *Calcarina* remains; in the Urgo-Aptian *Orbitolina* is the chief rock-builder; in the Upper Cretaceous *Alveolina*.

The maximum development of the Foraminifera falls in the Tertiary period. Massive beds of the Eocene Calcaire Grossier occurring in the Paris basin and in the Pyrenees, and affording an excellent building material, are composed of *Miliolidae* remains; other Eocene limestones consist of *Alveolina*, *Operculina*, *Orbitolites*, and *Orbitoides* aggregations. But of far greater geological importance are the *Nummulites*, which occur in incredible abundance in the Eocene and Oligocene Nummulites-formations of the Mediterranean district, Asia Minor, and Eastern Asia.

During the late Tertiary the *Nummulites* almost entirely disappear; only *Amphistegina* continues as an occasional rock-builder, and from the middle and later Tertiary on, the Foraminifera fauna remains very nearly the same as now.[1]

[1] [Additional references to the Literature on *Protozoa*:
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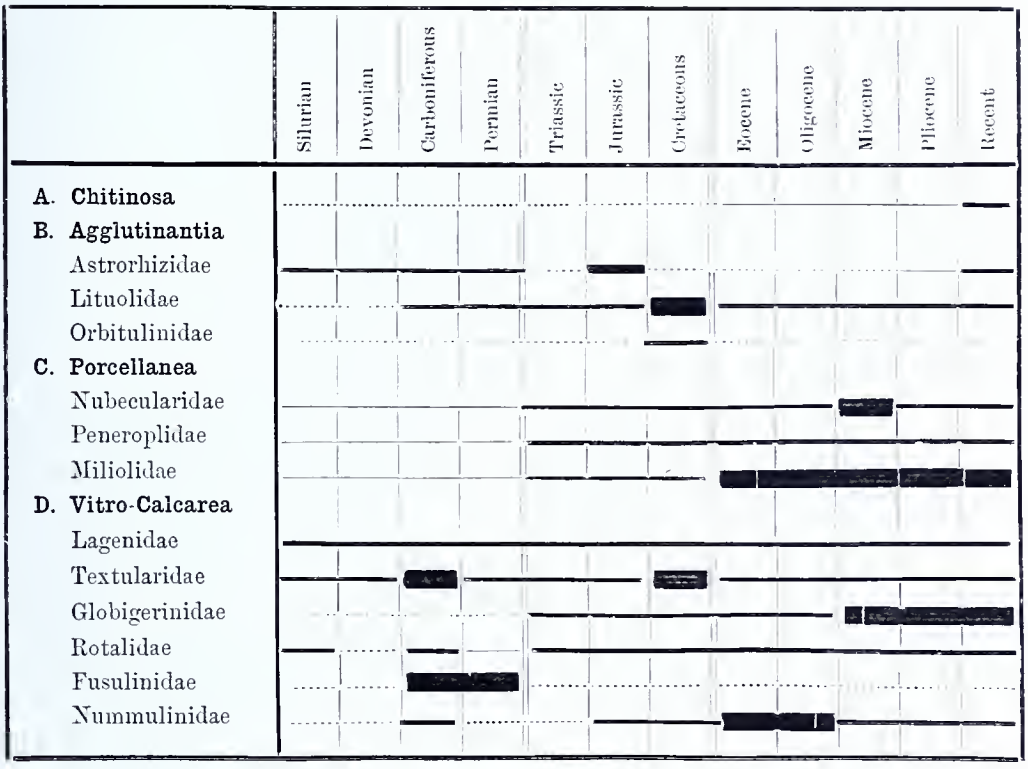
Very extensive bibliographies are contained in the works of Carpenter and Brady, cited on p. 19. Reference may also be made here to the exhaustive bibliography of the Sponges, which will be found in the monographs of Hinde and Rauff, cited on p. 42.—TRANS.]



Order 2. RADIOLARIA. Müller.[1]

(*Polycystina*, Ehrenberg.)

Marine Rhizopoda emitting fine, filiform, radially directed pseudopodia, with central capsule and extra-capsulum, and usually with delicate silicious skeleton.

The sarcode body of the Radiolarians is differentiated into (1) an inner central sphere or capsule of tough slimy protoplasm containing one or more nuclei, vacuoles, alveoles, granules, oil-globules, and sometimes crystals, and surrounded by a capsule-membrane perforated by pores or pylae; and (2) an outer jelly-like extra-capsulum, the sarcode of which emits pseudopodia. The individuals lead usually an isolated existence, and are only rarely united in colonies.

Most Radiolarians secrete skeletons composed either of bars or spicules of acanthine (an organic substance allied to horn or chitin) or silica, or they build an exceedingly delicate lattice-work composed of transparent amorphous silica. Only the latter forms are known in a fossil state, and owing to their minute size, are commonly indiscernible except with the aid of the microscope.

[1] *Ehrenberg, C. G.*, Mikrogeologie, 1854, and Abhandlg. Berliner Akad. 1875 (Radiolaria from Barbados).—*Haeckel, E.*, Die Radiolarien. Monograph 1862, and Report on the Radiolaria collected by H.M.S. *Challenger*, 1887.—*Hertwig, R.*, Der Organismus der Radiolarien, 1879.—*Stöhr, E.*, Palaeontographica, XXVI. 1878 (Radiolaria from Sicily).—*Rüst, D.*, Palaeontographica, XXXI. 1885, XXXIV. 1888, and XXXVIII. 1892.—*Dreyer, F.*, Die Tripoli von Caltanisetta. Jenaische Zeitschrift f. Naturw. XXIV. 1890.—*Cayeux, L.*, Bull. Geol. Soc. France, 1894, p. 197.

Haeckel divides the Radiolaria into four sub-orders, as follows :—

A. *Acantharia.*—Capsule-membrane uniformly perforated; skeleton composed of acanthinic spicules. Unknown in fossil state.

B. *Spumellaria.*—Capsule-membrane single, pores distributed all over; skeleton silicious, spherical, or discoidal, sometimes wanting (Fig. 48).

C. *Nasselaria.*—Capsule-membrane single, perforated only about the oral pole; skeleton silicious, helmet- or cap-shaped, conformation of poles dissimilar (Figs. 49, 50).

D. *Phaeodaria.*—Capsule-membrane double, perforated by one main opening prolonged into a tubulus, and by a few smaller accessory openings. A dark

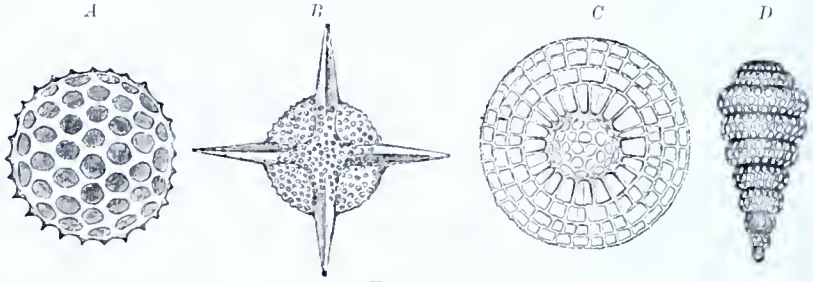


Fig. 46.

Silurian and Devonian Radiolarians: *A*, *Cenosphaera macropora*, Rüst. Ordovician; Cabrières, Languedoc. *B*, *Staurolonche micropora*, Rüst. Ordovician; Cabrières. *C*, *Caryosphaera Grobbecki*, Rüst. Upper Devonian; Schabenholz, near Elbingerode, Harz Mountains. *D*, *Lithocampe Tschernytschewii*, Rüst. Devonian; Ural. Magnified 100—120 diameters (after Rüst).

pigment body (*phaeodium*) constantly present in extra-capsular sarcode. Skeleton commonly consisting of hollow silicious spicules disposed in flask-shaped or variously shaped frameworks. Unknown in fossil state.

Radiolarians are exclusively marine organisms, and are found at all bathymetric zones. They occur in vast numbers, especially in tropical seas,

Fig. 47.

Carboniferous, Jurassic, and Cretaceous Radiolarians: *A*, *Stauracontium inaequale*, Rüst. Carboniferous; Sicily. *B*, *Trochodiscus Nicholsoni*, Rüst. Carboniferous; Harz. *C*, *Xiphodictya acuta*, Rüst. In coprolite from Lias; Hsede, Hanover. *D*, *Hymeniastrum rotundum*, Rüst. In coprolite from Cretaceous; Zilli, Saxony.

swimming on the surface, as well as at medium and even abysmal depths; particularly between 2000—4000 fathoms in depth, extensive deposits of "Radiolarian mud" have been found, the composition of which is largely silica with a small percentage of carbonate of lime.

The diversity of form exhibited by Radiolarians is most astonishing, and the identification of their microscopic silicious skeletons is impossible without

the aid of special literature. Contrary to formerly accepted ideas, the geological antiquity of the Radiolarians is very great; and they also play an important part in the composition of many silicious and calcareous-silicious rocks (quartzites, hornstone, jasper, phyllites, Aptychenschiefer, etc.) According to Barrois they are the oldest known animal organisms, since the Spumellaria (*Monosphaeroidae*) occur plentifully in the bituminous quartzites of Bretagne, interbedded with pre-Cambrian gneiss.

Although the group is still very imperfectly known, yet, according to Rüst, fossil Radiolaria are by no means less abundant and less diversified than the recent. Only in exceptional instances (Miocene of Barbados, Oran, Sicily) have the skeletons been preserved unaltered, and still consist of amorphous silica. In the older rocks the silica has usually become dissipated in the matrix, being replaced by lime carbonate, iron, or some colouring agent; in other cases the quartz has become cryptocrystalline, or replaced by a calcite pseudomorph.

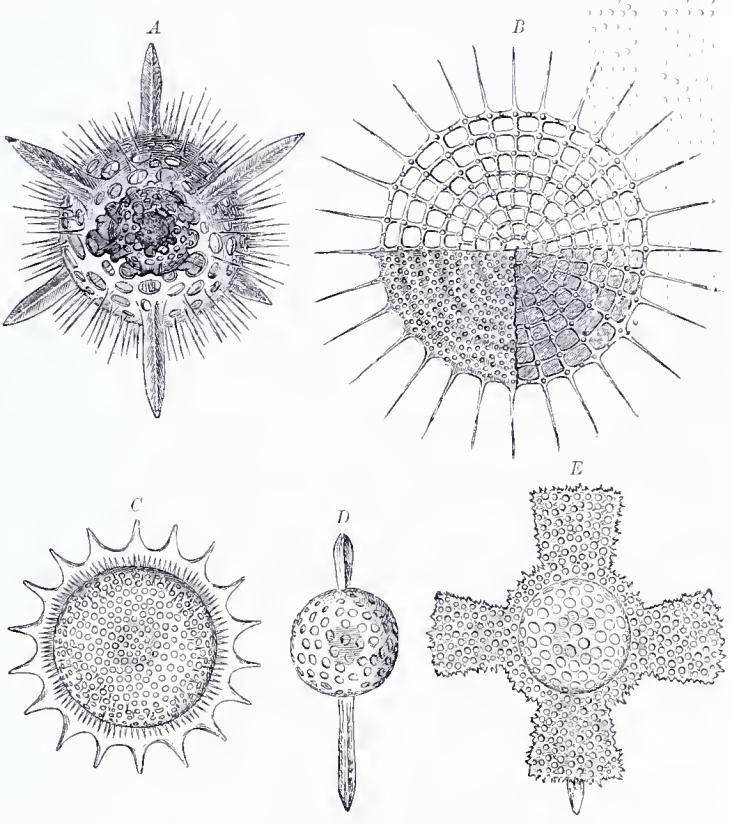


FIG. 48.

Recent and Tertiary Spumellarians: *A*, *Actinomma asteracanthium*, Haeck. Recent; Messina. *B*, *Stylodictya multispina*, Haeck. Recent; Messina. *C*, *Heliodiscus Humboldti*, Ehrbg. Barbados earth (Miocene); Barbados. *D*, *Haliomma dixiphos*, Ehrbg. Miocene marl; Caltanisetta, Sicily. *E*, *Astromma Aristotelis*, Ehrbg. Miocene; Barbados.

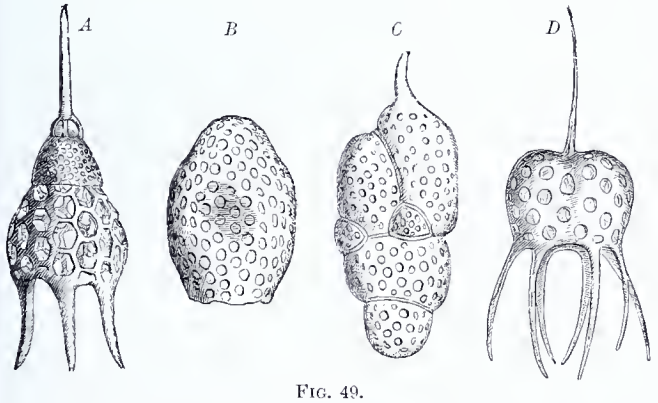


FIG. 49.

Recent and Tertiary Nasselarians: *A*, *Podocyrtis Schomburgki*, Ehrbg. Tertiary marl; Barbados. *B*, *Cyrtocalpis amphora*, Haeck. Recent; Messina. *C*, *Bothryocampe hexathalamia*, Haeck. Recent; Mediterranean. *D*, *Petalospyris foreolata*, Ehrbg. Tertiary marl; Barbados.

The Cambrian Griffelschiefer of Sonneberg in Thuringia contain poorly preserved *Sphaeroidea;* the usually dark, though sometimes red or light-coloured Ordovician strata of Langenstriegis in Saxony, and of Rehau and Steben in Franconia, the red jasper of Abington, Scotland, and the Ordovician silicious

rocks of Cabrières in Languedoc, are more or less rich in Radiolarian remains belonging exclusively to the *Spumellaria* (Fig. 46, *A*, *B*).

From the Devonian jasper of Siberia, the silicious schists of Hesse and Nassau, and the manganiferous quartzite of Elbingerode in the Harz, and other places, Rüst has described forty-six Spumellarian species and seventeen Nasselarian (*Cyrtoidea*). The sub-Carboniferous quartzites, phyllites, adinole, and jaspers from the Harz (Culm formation), Ural district, and Sicily have yielded 155 species, of which thirty-six belong to the *Nasselaria*. In general the Palæozoic Radiolarians are remarkable for their relatively large size and excellent preservation.

The Triassic appears to be destitute of Radiolarians except in the Alps, where they are abundant in the hornstone and silicious limestone of the Buchenstein beds of Hungary, and occur less frequently in the Reifling limestones, in the Wengen beds of Storzic in Krain, in the marls of St. Cassian, and in the silicious limestone of the Röthelstein, near Aussee, etc. They are usually associated here with the remains of sponges and Foraminifera. In the silicified coprolites of the Lias, found at Ilsede, Hanover, Radiolarians are very common; they are somewhat less frequent in the limestones of the Lower Lias on the Schafberg in Upper Austria. Certain hornstone beds of Middle Jurassic age, found at Piszke, Hungary, the Upper Jurassic puddingstones of Cittiglio, near Laveno on Lago Maggiore, and numerous Tithonian jaspers, as well as the Alpine Aptychus beds, are charged with Radiolarians; here the *Nasselaria* are nearly as plentiful as the *Spumellaria*. The Lower Cretaceous (Neocomian) of Gardenazza has yielded but few forms; but, on the other hand, coprolites from the Gault, found near Zilli in Saxony, and Lower Cretaceous clay marls in Manitoba, Canada, as well as the Upper Cretaceous marls of Haldem in Westphalia, and Vordorf in Braunschweig, contain excellently preserved skeletons in greater or lesser abundance. Even the flinty concretions of the Upper Chalk sometimes contain them, although in a poor state of preservation. Certain Eocene hornstones in Italy, according to Pantanelli, are filled with Radiolarian remains, while in the Flysch they are also very profuse in some localities, although usually poorly preserved.

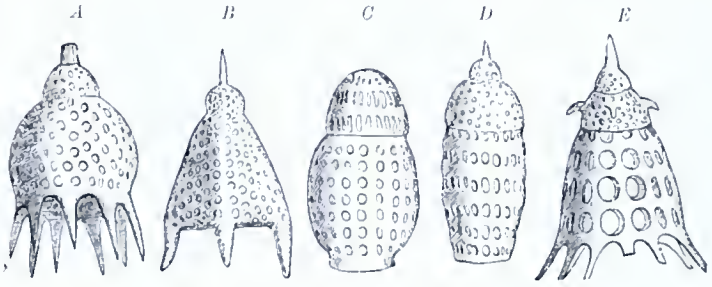


FIG. 50.

Tertiary Nasselarians from Barbados: *A*, *Anthocyrtis mespilus*, Ehrbg. *B*, *Lychnocanium Lucerna*, Ehrbg. *C*, *Dictyomitra Montgolfieri*, Ehrbg. *D*, *Eucyrtidium elegans*, Ehrbg. *E*, *Pterocodon campana*, Ehrbg.

By far the most noted occurrence of fossil Radiolarians is in the chalky "Barbados earth," of Miocene age, in which Foraminifera are also very conspicuous; while the "tripoli" of Grotte, Caltanisetta, and Girgenti in Sicily, of Oran, Aegina, Zante, the Nikobar Islands, and other localities (Miocene and Pliocene), is scarcely less noteworthy. Ehrenberg has described 278 species from Barbados alone, and from Sicily Stöhr has described 118 species, most of which belong to still extant Spumellarian, Nasselarian, and Phaeodarian genera.

Sub-Kingdom II. COELENTERATA. (Zoophytes)

Coelenterates or Zoophytes are free-swimming or attached aquatic animals of very variable form and size, with multicellular bodies, and more or less distinctly radial in symmetry. A large-sized mouth-opening conducts into a central gastric cavity (*gastrovascular space*), which either ends blindly, or is provided with peripheral pouches, or a canal-system for the conveyance of food-particles. Since the chief function of the gastrovascular space, together with its diverticula, is that of digestion, although including also the reproductive organs, it corresponds, at least physiologically, to the stomach and intestines of higher animals. A definite anal opening is absent; the excretions and sexual elements are voided through the mouth.

The body consists of three layers of cells, an ectoderm, mesoderm, and entoderm. The ectoderm often secretes a calcareous or horny skeleton, but in most cases the horny, silicious, or calcareous skeletal elements are the product of the mesoderm.

Reproduction is either sexual or asexual, or an alternation of generations may occur. The process of budding or self-division gives rise to polyzooid colonies, in which the individuals subsist in intimate relationships with one another, and sometimes institute a physiological division of labour.

R. Leuckart was the first to recognise the Coelenterates as constituting a distinct structural type of animals, and separated them from the Echinoderms, with which the older systematists had associated them under the general term of Radiates or Actinozoa. The Coelenterates are divided into three principal groups or sub-branches: *Porifera*, *Cnidaria*, and *Ctenophora*; of which only the first two have left traces in the rocks.

Sub-Branch I. Porifera. Hogg.

The Porifera or Sponges are sessile, aquatic animals of extremely variable form. The body consists of a single layer of pavement-cells forming the ectoderm, a likewise single layer of collared epithelial cells constituting the entoderm, and a strongly developed mesoderm tissue, which latter comprises the bulk of the soft parts (including all the organs, muscles, sexual elements, and nerves), and almost invariably secretes a hard skeleton. The latter may consist of horny sponge-fibres, or of regularly disposed silicious or calcareous skeletal elements. The whole body is ramified by a canal-system, and the outer epithelial layer is perforated by countless, minute, dermal pores for the entrance

of water laden with food-particles. The pores communicate by means of fine incurrent canals with sub-dermal ciliated chambers, from which larger excurrent canals conduct the water and sponge-food through the body, and generally open into a wide, exhalent opening called the *cloaca* or *paragaster*. Stinging cells, tentacles, and radial mesenteries are absent. The Porifera comprise but one class—the Sponges.

Class 1. SPONGIAE. Sponges.[1]

Sponges are remarkable for their extreme variability in external form and size; they lead either an isolated existence, or are united in colonies of cylindrical, tubulate, pyriform, fungus-like, bulbous, spherical, compressed, leaf-like, umbel-, bowl-, or beaker-shaped, or of botryoidal form. They are long or short stemmed, or a peduncle may be absent; sometimes the stock is branching, and the arms may be either separate or interlaced so as to form networks. Nothing is less stable than the outer conformation, which varies excessively according to the situation and other physical conditions, and whose systematic importance, accordingly, is very slight. The size is also extremely variable, ranging from that of a pin-head to 1½ metres in diameter.

Sponges are invariably sessile in habit, being attached either by means of a stem or a bundle of anchoring spicules, or they may be simply encrusting at the base.

The *canal-system* by which the whole body is traversed, is extremely complicated in thick-walled, but simple in thin-walled sponges. A distinction is recognised between incurrent or inhalent, and excurrent or exhalent canals.[2] The water enters through the dermal pores, and passes through the incurrent canals into the ciliated chambers, which are lined with epithelial cells. From these it is conveyed through all parts of the body by means of the frequently branching excurrent canals, which open into a sac-like, tube-like, or funnel-shaped cloaca. The exhalent opening of the latter is termed the osculum. Extremely thin-walled sponges have no cloaca, osculum, or branching canal-

[1] Literature: A. On recent Sponges.

Schmidt, O., Die Spongien des Adriatischen Meeres, Leipzig, 1864-66.—Die Spongien des Meerbusens von Mexico, Jena, 1879-80.—*Haeckel, E.*, Die Kalkschwämme, 1872.—*Schulze, F. E.*, Untersuchungen über den Bau und die Entwickelung der Spongien; Zeitschr. für wissenschaft. Zool., Bd. XXVII., XXVIII., XXX., 1876-80.—Report on the Hexactinellida; Sci. Results *Challenger* Exped., Zoology, vol. XXI. 1887.—*Vosmaer, G. C. J.*, Porifera; *Bronn's* Classen und Ordnungen des Thierreichs (2nd ed.), Bd. II. 1882-87.—*Leudenfeld, R. v.*, Das System der Spongien; Biolog. Centralblatt, Bd. IX. 1889.—A Monograph of the Horny Sponges, London, 1889.

B. On fossil Sponges.

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[2] [In the terminology proposed by Rauff (*tom. cit.*), inhalent canals are designated as *epirrhysa*, and exhalent canals *aporrhysa*; the former terminate on the periphery in *ostia* (not to be confounded with the finer dermal pores), while the latter terminate on the cloacal surface in *postica* (again not to be confounded with gastral pores). Postica are usually larger than ostia, and differ from them in form and arrangement.—TRANS.]

system, but the excurrent canals terminate directly in small openings situated on the upper surface of the body. The cloaca when present is often of considerable depth, although sometimes shallow, or reduced to a mere sac-like prolongation of the osculum. Forms with a large and deep cloaca are regarded as single individuals, those with numerous cloacae and oscula as colonies. But since all the cloacae of a colony communicate by means of canals, while the oscula are never surrounded by a crown of tentacles, it is often difficult to distinguish between large excurrent canals and true cloaca, and hence also between individuals and colonies.

Reproduction is either sexual or asexual. In the first process the fertilised ova complete a tolerably regular segmentation, develop into a gastrula, pass out through the osculum, and attach themselves to some foreign object. Asexual reproduction takes place by budding, the young buds remaining attached to the parent individual, and thus giving rise to colonies. Reproduction by means of fission is of rare occurrence.

The great majority of sponges secrete a skeleton composed either of horny fibres or of silicious or calcareous spicules, or they incorporate foreign bodies into their framework. Only a few recent forms (*Myxospongiae*) are without a skeleton. In the horny sponges (*Ceratospongiae*) the skeleton consists of anastomosing and reticulated fibres of spongin, an organic nitrogen compound resembling silk. The fibres are either solid, or they contain an axial canal, which is sometimes cored with foreign bodies, such as sand-grains, fragments of sponge-spicules, Foraminifers, Radiolarians, etc.

Silicious spicules are sometimes encased in horny fibres, sometimes occur detached in the cellular tissues, or are interwoven and consolidated with one another in various ways to form scaffoldings. In each genus the skeleton is composed of but a single form, or at the most of but a few regularly repeated varieties of silicious bodies, which are called the *skeletal elements*. In addition to these there occur more or less abundantly, especially on the outer surface and in the cloacal and canal walls, extremely delicate flesh-spicules, usually of small size and of great diversity of form. The flesh-spicules are as a rule destroyed during fossilisation. All the silicious skeletal elements are secreted by nucleated cells, and are composed of concentric layers of colloidal silica, deposited usually about a slender axial canal. In some spicules, notably those having spherical or stellate contours, the axial canal is wanting. It is very delicate in fresh spicules, but becomes enlarged by maceration, and in fossil specimens it is often coarsely calibrated.

The multitudinous varieties of silicious skeletal elements (Fig. 51) are resolvable into a few fundamental types, as follows :—

(*a*) Uniaxial spicules or *Monaxons* (Fig. 51^{1-10} and $^{14-16}$). Straight or bent, smooth, prickly or knotty, bevelled, sharpened or truncated needles, rods, hooks, clasps, pins, and anchors (*amphidiscs*). They invariably contain an axial canal, which may be either entirely sealed up, or open at one or at both ends.

(*b*) Tetraxial spicules or *Tetraxons* (Fig. 51^{17}). The normal form is characterised by four equal rays intersecting like the bisectrices of the plane angles of a regular tetrahedron. Triaxial forms result from the occasional abortion of one of the rays. One of the rays may become elongated or otherwise modified so as to form anchors (*triaens*) with three simple or furcate hooks (Fig. 51^{18-23}). Three of the rays may be numerously divided or foliately expanded so as to produce forms resembling thumb-tacks (*trichotriaens*, *phyllo-*

triaens); atrophy of the fourth ray in the last-named form reduces the spicule to a delicate silicious disk (Fig. 51[28]). A peculiar forking of the shaft gives rise to candelabras or *amphitriaens*, while other modifications may produce umbel-like spicules (Fig. 51[26]), etc.

Certain skeletal elements of the Lithistids (Figs. 53-68) may be regarded as irregular tetraxons (*desmoms*), in which the extremities of the four rays are prolonged in knotty, root-like excrescences, or in which, owing to the un-

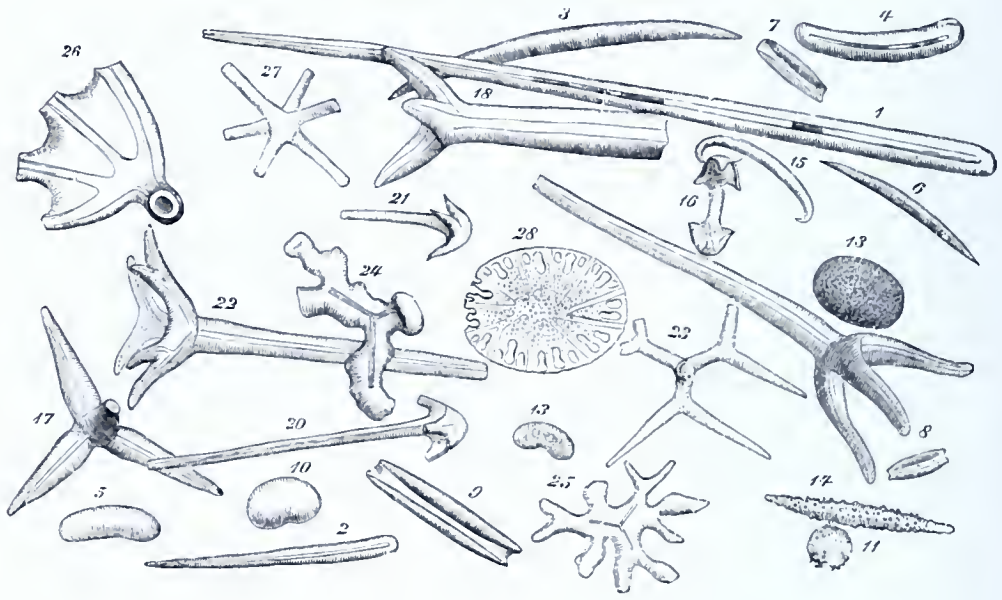

FIG. 51.

Various forms of Sponge spicules from the Upper Cretaceous of Haldem, Westphalia; magnified 25 diameters. 1—6, Uniaxial rods and needles. 7—9, Uniaxial silicious elements with coarse axial canals. 10—13, Uniaxial cylinders and spheres. 14, Microspined spicule. 15, Clasp-hook flesh-spicule. 16, Bispatulate flesh-spicule. 17, Regular four-rayed spicule (chevaux de frise). 18—21, Trifid anchor-shaped spicules. 22—23, Anchors with furcate head-rays. 24—25, Irregular four-rayed skeletal elements. 26, Umbel-shaped spicule. 27, Six-rayed spicule. 28, Polyaxile silicious disc.

symmetrical growth, branching, or atrophy of one or more of the arms, extremely irregular forms are produced; for these a special terminology has been devised by Ranff.

(*c*) Hexactinellid spicules (*Hexactins* or *Triaxons*) (Figs. 69-74). The ground-form is an axial cross with six equal arms intersecting at right angles like the axes of a regular octahedron. Atrophy of one or more of the rays may result in pentaxial, tetraxial, triaxial, or even nail-shaped forms, without their real character becoming entirely obliterated. Bifurcation or other modifications of a number or all of the rays produce those exquisite silicious structures so characteristic of the group *Hexactinellida*, which resemble candelabras, double-headed anchors, fir-trees, pitch-forks, rosettes, etc. The fusion of juxtaposed hexactins produces more or less symmetrical latticeworks with cubical interstices.

(*d*) Anaxile or polyaxile bodies of spherical, cylindrical, stellate, or discoidal shape, which are not derivable from either of the three ground-forms, occur in only a few varieties of recent and fossil silicious sponges.

Calcareous skeletal elements are much less complicated, and are generally smaller and more perishable than the silicious. Their form is either triaxial (*triods*), tetraxial (*tetraxons*), or nail-shaped (*monaxons*). The triaxial and

tetraxial spicules are very rarely forked or otherwise modified. Each skeletal element behaves optically like a single calcite crystal; axial canals are absent.

The skeletal elements in sponges are arranged chiefly with reference to the circulation of water through the canal-systems. In thin-walled forms they are more or less closely crowded together, and are often regularly oriented in the soft parts; in other forms they are encased in horny fibres, or are packed in between the canals; in still others they are united to form an irregular framework, or may be soldered together in a regularly reticulated scaffolding.

The horny fibres are totally destroyed during fossilisation; calcareous spicules are often wholly or partially dissolved, or are replaced by infiltrating lime carbonate, and assume a dense fibrous appearance (*Pharetrones*). In silicious sponges also the skeletal elements are rarely preserved unaltered; as a rule the originally colloidal silica becomes crystalline, or is dissolved and carried away. The cavities thus formed may subsequently become filled with infiltrating quartz, limonite, or most commonly with carbonate of lime. In this manner the skeletons of fossil silicious sponges are converted into calcite, and, contrariwise, spicules that were originally calcareous may become silicified. Hence the distinction between silicious and calcareous sponges in the fossil state depends entirely upon morphological characters, and not at all upon the chemical composition of the preserved parts.

Sponges are divided into four sub-classes:—*Myxospongiae*, *Ceratospongiae*, *Silicispongiae*, and *Calcispongiae*. The latter group stands in sharp contrast to the other three, which are connected by intermediate forms, and constitute together a group of equal value with the calcareous sponges. Skeletal elements are absent in the *Myxospongiae*, whose bodies are composed entirely of soft cellular tissues. The *Ceratospongiae* also lack imperishable hard parts, the spongin fibres being entirely destroyed during fossilisation. The reputed horny sponges from the Trias (*Rhizocorallum*), Jurassic, and Cretaceous (*Spongites*, *Saxonicus*, *Paramudra*, etc.) are either of inorganic nature, or are zoologically indeterminate. All fossil sponges, therefore, belong either to the *Silicispongiae* or the *Calcispongiae*. The oldest forms are found in the Cambrian; in the Trias, Jurassic, and Cretaceous they are very abundant.

Sub-Class 3. **SILICISPONGIAE**. Silicious Sponges.

Skeleton composed either exclusively of silicious elements, or of horny fibres enclosing silicious spicules.

Order 1. MONACTINELLIDA. Zittel.

(*Monaxonia*, F. E. Schulze.)

All skeletal elements uniaxial.

The *Monactinellida* include the majority of existing marine sponges, most of which occur at moderate depths; and also the few fresh-water forms (*Spongilla*) that are known. The skeleton, as a rule, is composed like that of the horny sponges, of anastomosing spongin fibres, which either encase rod-like spicules, or contain quantities of uniaxial silicious elements; sometimes the latter are also present in the soft parts. In each genus there are generally but one or but a few varieties of silicious elements present, which are uniformly dis-

tributed throughout the body. Needles, hooks, crotchets, cylinders, spindles, amphidiscs, and the like occur in great diversity. Owing to the decomposition of the horny fibres during fossilisation, and the fact that the skeletal elements are never soldered together, the latter become detached and strewn in all directions. While Monactinellid spicules are very common in certain formations, they are rarely united in the form of coherent skeletons, and are only capable of generic determination when possessing characteristic forms (*Renieria*, *Esperia*, etc.) The lowermost members of the Alpine Lias often contain considerable hornstone, and are sometimes completely filled with rod-shaped spicules. In various Cretaceous and Tertiary horizons also Monactinellid spicules are enormously abundant. Hinde has described a *Climacospongia* from the Silurian of Tennessee, in which the skeleton consists of spicules arranged in longitudinal rows, and connected by transversely disposed elements. The spicules were probably originally enclosed in horny fibres. The *Clionidae* secrete pin-shaped silicious elements which are also encased in horny fibres, and by means of which they bore labyrinthic passages in the shells of mollusks. Fossil sponge-borings are also common. Detached spicules of *Renieria*, *Axinella*, and *Haplistion* have been described by Hinde from the English Carboniferous Limestone.

Order 2. TETRACTINELLIDA. Marshall.

(*Tetraxonia*, F. E. Schulze.)

Skeleton composed of regular tetraxons which are generally combined with uniaxial, polyaxile, or heteraxile silicious bodies. The skeletal elements occur detached throughout the soft parts, and are never united to form a connected framework.

Fig. 52.

Tethyopsis Steinmanni, Zitt. Upper Cretaceous; Ahlten, Hanover. $\frac{14}{1}$.

The most common forms of skeletal elements are normal tetraxons, anchors with simple or furcate prongs, spheres, and stellate bodies. In certain genera (*Geodia*) the large anchors and cylinders are disposed in radiately arranged fascicles, and are surrounded by a thick layer of anaxile spheres.

Detached Tetractinellid spicules associated with Monactinellids occur more or less abundantly in the Carboniferous Limestone, the Alpine Infra-Lias, the English Neocomian, the Deister Sandstone (Hils), the Upper Cretaceous of Haldem and Coesfeld in Westphalia, and in the Tertiary and Pleistocene formations. The skeletal elements are preserved in their natural position in the genera *Ophiraphidites*, Carter; *Tethyopsis*, Zittel (Fig. 52); and *Pachastrella*, Schmidt.

Order 3. LITHISTIDA. Schmidt.

Massive, thick-walled, silicious sponges, usually with complicated canal-system. Skeleton composed of irregular tetraxons or monaxons (desmoms), which develop knotty or root-like branches either at the extremities or all along the shaft, and are firmly

united by zygosis. Symmetrical, tetraxial, uniaxial, or polyaxile dermal and flesh-spicules also present.

The Lithistids are closely related to the Tetractinellids, and, in the opinion of many zoologists, constitute with them but a single order.

The Lithistids are peculiarly well suited for preservation, owing to the massive, stony character of their skeletons; and their remains occasionally form thick deposits, especially in the Jurassic and Cretaceous. Their outer configuration is extremely variable; most commonly it is bowl-shaped, cup-shaped, pyriform, globular, bulbous, or plate-like; while the body is attached either by the base or by means of a peduncle. The canal-system varies greatly in different genera, but is usually well developed and more or less complicated. The four-rayed skeletal elements are interlocked by means of the root-like branching ends of the rays, and the points of intersection (*nodes*) with the ends of adjacent uniaxial spicules are thickened into balls. The uniaxial, usually very irregular skeletal elements are interlaced on all sides by means of root-like processes. Dermal and flesh-spicules are preserved only under exceptionally favourable conditions, but are invariably present in recent genera, and furnish valuable systematic characters. The classification of fossil Lithistids is based wholly upon the skeletal elements and canal-systems. Five principal groups are recognised, whose subdivision into families need not concern us at present:—*Tetracladina*, *Eutaxicladina*, *Anomocladina*, *Megamorina*, and *Rhizomorina*. Existing Lithistids occur most abundantly at depths ranging between 100 and 400 metres, but are occasionally found as deep as 1800 metres.

Sub-Order A. TETRACLADINA. Zittel.

Skeletal elements composed of four usually equal rays, each of which encloses an axial canal, and has extremities terminating in root-like strands or processes; the spicules are intertwined to form an open meshwork. Dermal spicules either grapnel-like tetraxons, frequently with furcate prongs, or discoidal with entire or lobate margin; or they are nail-shaped or cylindrical monaxons.

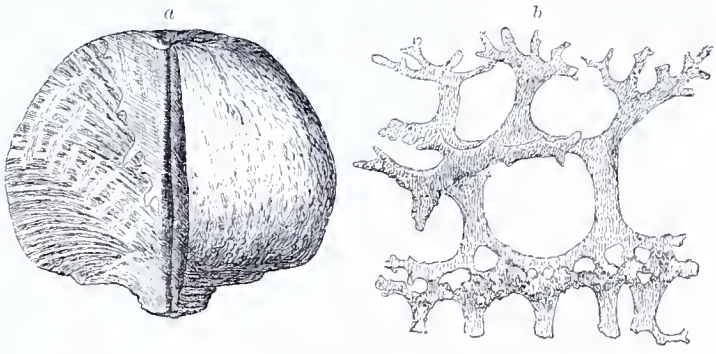

Fig. 53.

Aulocopium aurantium, Oswald. Diluvium; Sadowitz, Silesia. *a*, Individual in $^1/_2$ natural size; *b*, Skeleton magnified 60 diameters.

The skeletal elements of the *Tetracladina* are usually symmetrical tetraxons, whose four smooth, more rarely tuberculate or knotty rays intersect approximately at an angle of 109½°. They occur in the Cambrian and Silurian, are very scarce in the Upper Jurassic (*Protetraclis*), but common in the Cretaceous, Tertiary, and Recent periods.

Aulocopium, Oswald (Fig. 53). Hemispherical or bowl-shaped with short peduncle; inferior surface covered with dense, wrinkled, silicious skin. Cloaca central; sponge body with numerous arched canals parallel to contour of peri-

phery, and with finer radial canals leading from exterior to cloaca. Skeleton composed of irregular smooth-rayed tetraclons with root-like branching

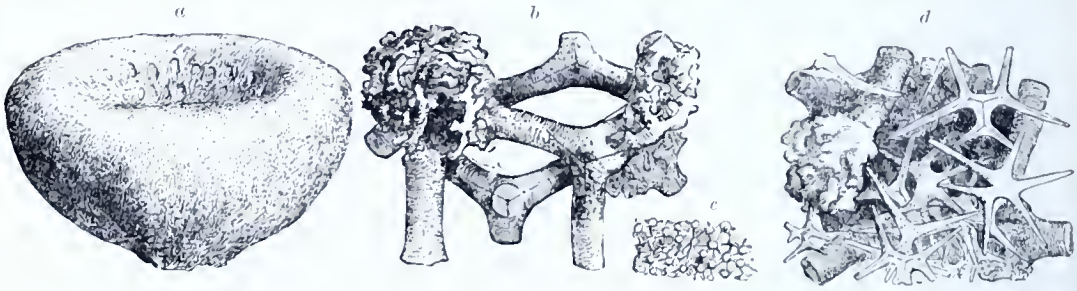

Fig. 54.

Callopegma acaule, Zitt. Senonian; Ahlten, Hanover; *a*, Individual in $^3/_4$ natural size; *b*, Skeleton magnified $^{40}/_1$; *c*, Portion of periphery, $^2/_1$; *d*, Same magnified $^{40}/_1$, and showing anchors with furcate head-rays.

extremities, disposed in rows parallel to the radial canals. Occurs (usually replaced by calcite) in the Ordovician of the Russian Baltic Sea Provinces,

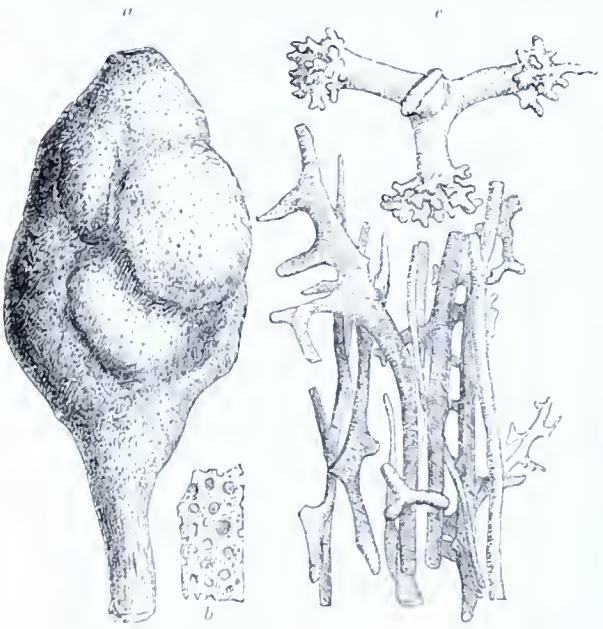

Fig. 55.

Phymatella tuberosa, Quenst. sp. Quadratenkreide (Upper Senonian); Linden, near Hanover. *a*, Sponge, $^1/_2$ natural size; *b*, Outer surface, $^1/_1$; *c*, Skeletal element, $^{50}/_1$; *d*, Spicules from stalk portion, $^{50}/_1$.

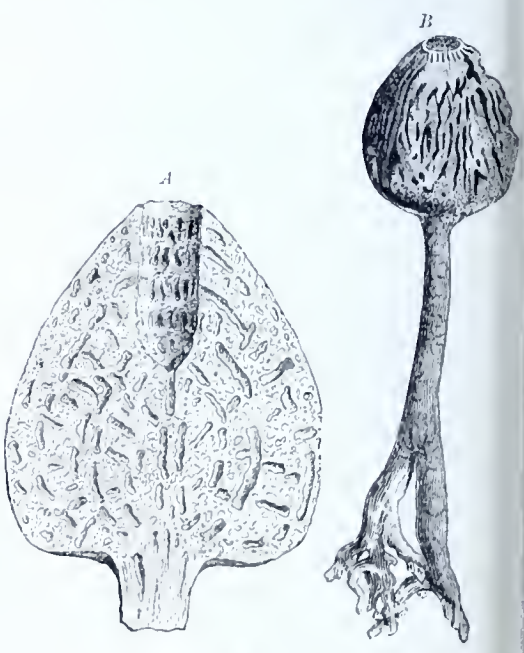

Fig. 56.

Siphonia tulipa, Zitt. Greensand; Blackdown. *A*, Longitudinal section, natural size. *B*, Sponge with peduncle and root, $^1/_2$ natural size (after Sowerby).

Ordovician of Illinois, and Silurian of Gottland. Also in erratic blocks on the plains of Northern Germany, usually chalcedonised.

Archaeoscyphia, Hinde. Cambrian.

Callopegma, Zittel (Fig. 54). Bowl- or funnel-shaped, short-stemmed, thick-walled. External surface perforated by smaller, internal by larger canal-openings (ostia and postica). Skeleton composed of smooth-rayed tetraclons, the digitate extremities of which are inflated into balls. Dermal spicules in the form of anchors and rods. Upper Cretaceous.

Phymatella, Zittel (Fig. 55). Upper Cretaceous.

Siphonia, Park. (Fig. 56). Fig-, pear-, or apple-shaped, with long or short pedunele. Body with deep cloaca, into which arched canals running parallel with the periphery, together with numerous fine radial canals, conduct. Skeleton composed of smooth-rayed, branching dichotriders. Dermal spicules

Fig. 57.

Jerea pyriformis, Lamx. Greensand; Kelheim, Bavaria. $^1/_2$ natural size.

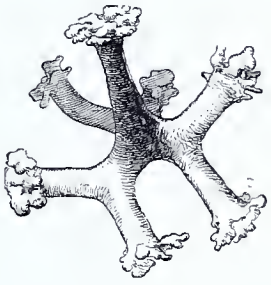

Fig. 58.

Skeletal element of *Jerea Quenstedti*, Zitt., showing branching extremities of rays. Quadratenkreide; Linden, near Hanover. $^{40}/_1$.

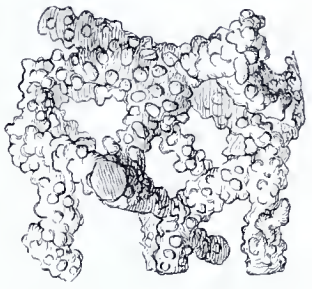

Fig. 59.

Plinthosella squamosa, Zitt. Skeleton magnified 80 diameters. Senonian; Ahlten, Hanover.

in the form of monaxons and graphnels. Abundant in Middle and Upper Cretaceous.

Hallirhoa, Lamx. Like the preceding, but invariably short-stemmed. Body pyriform and lobate, owing to a number of deep constrictions. Cenomanian.

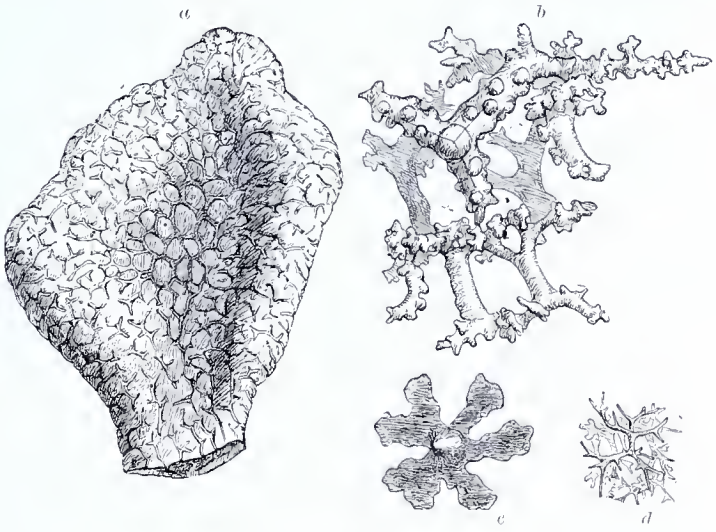

Fig. 60.

Rhagadinia rimosa. Roem. sp. Senonian; Ahlten, Hanover. *a*, Sponge, $^2/_3$ natural size; *b*, Skeleton, $^{40}/_1$; *c*, Lobate disk from dermal layer, $^{40}/_1$; *d*, Spicule of dermal layer, $^{40}/_1$.

Jerea, Lamx. (Fig. 57). Body pyriform, flask-shaped or cylindrical, with truncate or depressed summit, in which a number of tube-like canals, vertical in the central portion but arched in the peripheral, terminate. Crossing the latter are finer radial canals. Skeleton composed of tetraclons and dichotriders. Common in Middle and Upper Cretaceous.

Polyjerea, From., *Astrocladia*, *Thecosiphonia*, *Calymmatina*, Zitt., *Turonia*, Mich., *Plinthosella*, Zitt. (Fig. 59). Cretaceous. *Discodermia*, Boc., *Rhacodiscula*, Zitt., etc. Cretaceous and Tertiary.

Rhagadinia, Zittel (Fig. 60). Ear-, plate-, or bowl-shaped, short-stemmed. Both surfaces traversed by irregular branching furrows, in which the canalicular ostia are situated. Skeletal elements four-rayed, sometimes uniformly

or only distally covered with tuberculous knobs, and with digitate extremities. Dermal spicules in the form of six-lobed disks provided with a short shaft, and minute, multifid tetraclons. Upper Cretaceous.

Sub-Order B. EUTAXICLADINA. Rauff.

Skeleton composed of four-rayed spicules with three equally developed simple or bifurcate rays which terminate distally in root-like fibres; and one foreshortened, inflated fourth ray (ennomolcon). Axial canals probably in all of the rays. Skeletal elements invariably arranged in either parallel or alternating rows, and united by zygosis into a network with triangular or irregular meshes; spicular nodes greatly inflated.

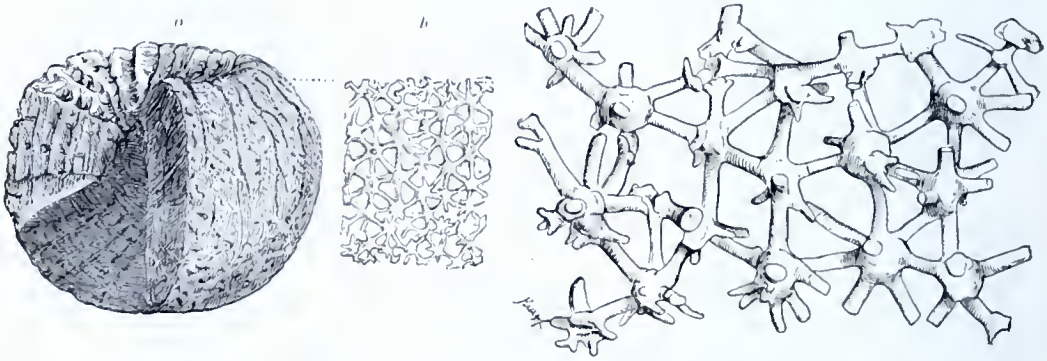

Fig. 61.

Astylospongia praemorsa, Goldf. sp. In erratic from Mecklenburg. *a*, Sponge, partially cut into, natural size; *b*, Skeleton, $^{12}/_{1}$; *c*, Portion of same highly magnified.

Nearly all the genera are Silurian; a few (*Mastosia*, *Lecanella*) occur in the Upper Jurassic.

Astylospongia, Roem. (Figs. 61, 62*a*). Spherical, with shallow depression on the summit; base evenly rounded, unattached; probably fastened by means of anchoring fibres. Large-sized canals directed parallel to periphery in the outer portion of the body, vertical in central portions; besides these are numerous fine radial canals which terminate in pores all over the periphery. Skeletal elements with four smooth elongated rays, one or all of which branch dichotomously just above the junction with the shorter arm. Spicular nodes thickened into large knots. Ordovician of the Russian Baltic Sea Provinces, and Silurian of Sweden and North America (notably in Tennessee), usually chalcedonised. Also in erratics in the Diluvium of Northern Germany.

Fig. 62.

a, Detached skeletal element of *Astylospongia*, $^{120}/_{1}$; *b*, Detached skeletal element of *Hindia*, $^{80}/_{1}$ (after Rauff).

Caryospongia, *Carpospongia*, Rauff. Ordovician and Silurian; Europe.

Palaeomanon, Roem. (*Astylomanon*, Rauff). Like *Astylospongia*, but bowl-shaped, with shallower and wider cloacal depression. Entire surface covered with pores. Silurian; North America. *P. cratera*, Roem.

Caryomanon, *Carpomanon*, Rauff. Silurian; North America.

Hindia, Duncan (Fig. 62*b*). Body spherical, with perforate periphery, traces of attachment wanting. All canals radiate from the centre outward. Skeletal elements composed of three simple rays beset with prickly tubercles, and a reduced button-like fourth arm. All spicules regularly disposed in rows parallel with radial canals. Silurian; North America.

Sub-Order C. ANOMOCLADINA. Zittel.

(*Didymmorina*, Rauff.)

Skeletal elements composed of short, smooth rays with spherically inflated ends which give off three, four, or more simple or digitate branches; the latter are united by zygosis with processes of adjacent rays; axial canals simple. Dermal spicules rod-shaped monaxons. Upper Jurassic and Recent.

Cylindrophyma, Zitt. (Fig. 63). Body cylindrical, thick-walled, attached; cloaca wide and tube-like, receiving numerous radial canals, and extending

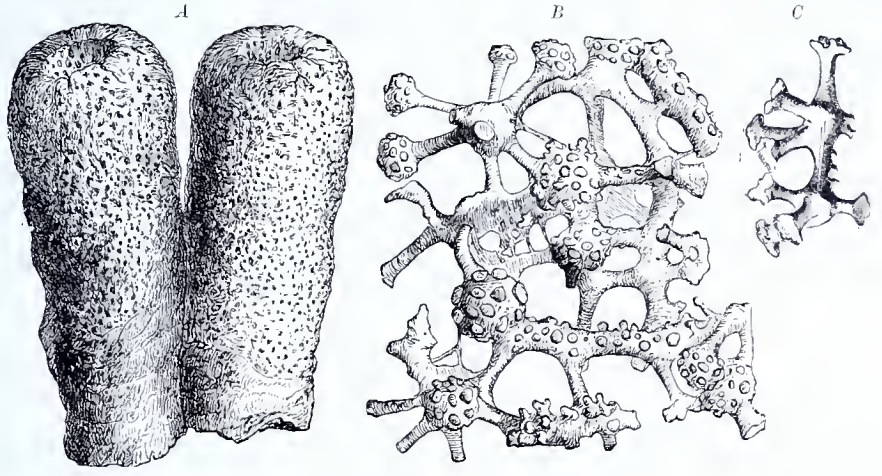

FIG. 63.

Cylindrophyma milleporata, Goldf. sp. Upper Malm; Hochstrass. *A*, Two individuals, $^1/_2$ natural size. *B*, Skeleton magnified 30 diameters. *C*, Detached skeletal element of *Cylindrophyma*, $^{60}/_1$ (after Rauff).

down as far as the base. External surface perforated by fine ostia. Common in Upper Jurassic. 2b!c9

Melonella, Zitt. Skeleton apple-shaped or hemispherical, with broad base, or provided with very short peduncle; base covered with wrinkled silicious skin. Cloaca deep, funnel-shaped. Coarser canals arched, parallel with periphery; finer incurrent canals radially directed. Upper Jurassic. *M. radiata*, Quenst. sp.

Sub-Order D. MEGAMORINA. Zittel.

(*Rhabdomorina*, Rauff.)

Usually large-sized, elongated, smooth, bent, loosely interlocking, irregularly branching, or only terminally forked skeletal elements with simple axial canals; interspersed among which small, radiciform, numerously branching elements (rhizomorins) are occasionally present. Dermal spicules uniaxial or grapnel-shaped. Ordovician, Silurian, Carboniferous, Jurassic, Cretaceous, and Recent.

Saccospongia, Rauff. Silurian. *Megalithista*, Zitt. Upper Jurassic; Nattheim.

Dorylerma, Zitt. (Fig. 64). Sponge-body cylindrical, simple or branching, pyriform or compressed, with a number of larger canals running parallel with the body axis, and numerous smaller radial canals. Skeletal elements large, bent, and divided into two or more simple branches. Dermal spicules in the form of three-fluked anchors. Upper Cretaceous; Northern Germany, England, and France. According to Hinde, also Carboniferous.

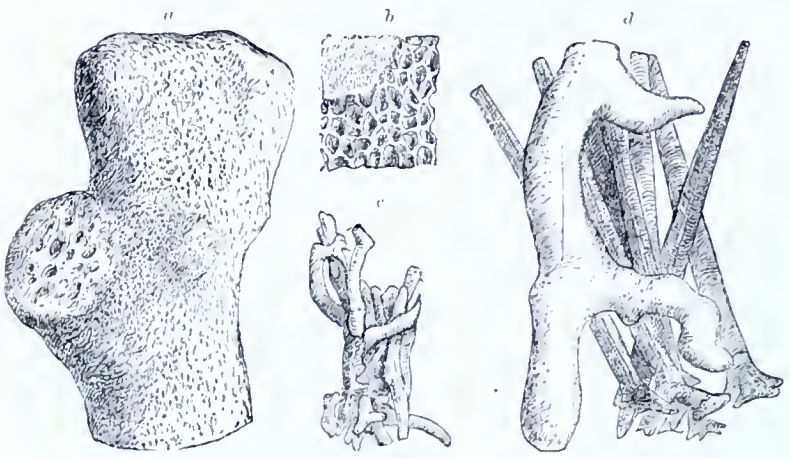

FIG. 64.

Dorylerma dichotoma, Roem. sp. Upper Cretaceous. *a*, Sponge, natural size; *b*, Dermal layer, $^2/_1$; *c*, Bundle of skeletal elements, $^{10}/_1$; *d*, Skeletal element and several dermal spicules with furcate, anchor-shaped head-rays, $^{30}/_1$.

Carterella, Zitt. Cretaceous.

Isorhaphinia, Zitt. Sub-cylindrical, pedunculate, with wide cloaca reaching nearly to the base. Skeletal elements large, slightly bent, rod-shaped, inflated at the ends, rarely dichotomously branching. They are associated in bundles, and so interlocked at their extremities as to form an open meshwork. Cretaceous. *I. texta*, Roemer sp.

Sub-Order E. RHIZOMORINA. Zittel

Skeletal elements small, composed of four or of three principal rays, or simple and irregular, with numerous projecting spines or tubercles; axial canal simple or branching. Dermal spicules monaxons, tetraxons, or similar to those of the skeleton. Chiefly Jurassic, Cretaceous, and Recent.

?Nipterella, Hinde. Cambrian.

Cnemidiastrum, Zitt. (*Cnemidium*, p. p. Goldf.), (Fig. 65). Turbinate or bowl-shaped, with deep cloaca. Walls thick, perforated by numerous radial canals disposed in tiers one over another, thus forming vertical fissures which often divide toward the exterior. Skeletal elements irregularly branching, entirely beset with blunt, spiny processes. Abundant in the Upper Jurassic Spongitenkalk of South Germany, the skeletons being almost invariably replaced by calcite. *C. rimulosum*, Goldf. According to Hinde also present in the Carboniferous Limestone of Ireland.

Hyalotragos, Zitt. Bowl-, plate-, or funnel-shaped, with short peduncle. Depression in summit perforated by the ostia of numerous short canals. External surface finely perforate, or covered by a smooth or wrinkled dermal layer. Skeletal elements irregular, with numerous branches beset with points, but with few spines. Very abundant in Upper Jurassic Spongitenkalk. *H. patella*, Goldf. sp.

Platychonia, Zitt. Leaf- or ear-shaped, irregularly undulating, covered on both surfaces with fine pores. Skeletal elements resembling those of *Hyalotragos*. Upper Jurassic. *P. vagans*, Quenst. sp.

Jereica, Zitt. (Fig. 66). Sponge cylindrical, turbinate, pyriform, or club-shaped, with short peduncle. Summit truncated or with shallow depression, perforated by the postica of vertical excurrent canals. Exterior perforated by

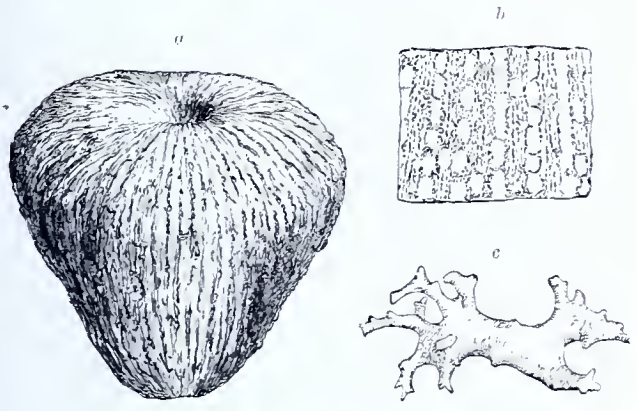

FIG. 65.

Cnemidiastrum stellatum, Goldf. sp. Upper Jurassic Spongitenkalk; Hossingen, Württemberg. *a* Sponge, 1/2 natural size; *b*, Vertical tangential section, showing radial canals in vertical clefts: *c*, Skeletal elements, 60/1.

FIG. 66.

Skeleton of *Jereica polystoma*, Roem. sp. Upper Cretaceous; Ahlten, Hanover. 60/1.

ostia of the finer radial incurrent canals. Skeletal elements root-like, bent, irregularly branching, with numerous short lateral processes. Upper Cretaceous. *J. polystoma*, Roem. sp.: *J. punctata*, Goldf. sp.

Chenendopora, Lamx. (Fig. 67). Goblet-, funnel-, or bowl-shaped, with

FIG. 67.

Chenendopora fungiformis, Lamx. Senonian; Chatellerault, Touraine. 1/3 natural size.

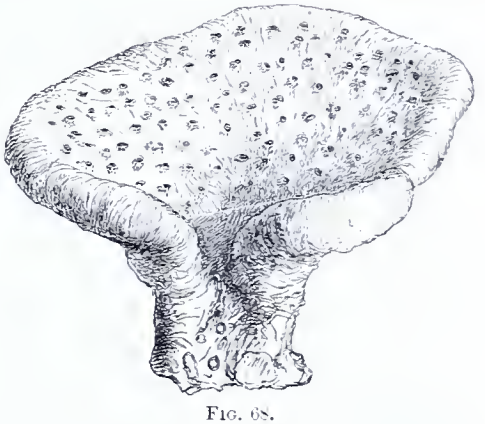

FIG. 68.

Verruculina auriformis, Roem. sp. Quadratenkreide; Linden, near Hanover. 2/3 natural size.

peduncle. Cloaca deep, perforated by postica of fine canals. Skeletal elements numerously branched, and containing branching axial canal. Upper Cretaceous.

Verruculina, Zitt. (Fig. 68). Foliate-, funnel-, ear-, or bowl-shaped, short-stemmed or sessile. Ostia on the upper surface surrounded by slight, collar-like elevations. Middle (Gault) and Upper Cretaceous.

Amphithelion, Zitt. Like the preceding, but with both ostia and postica terminating in bosses. Cretaceous.

Other genera: *Seytalia*, *Coelocorypha*, *Stachyspongia*, *Pachinion*, *Seliscothon*, Zitt. etc., in the Middle and Upper Cretaceous.

Order 4. HEXACTINELLIDA. O. Schmidt.

(*Triaxonia*, F. E. Schulze.)

Silicious sponges with six-rayed skeletal elements, the rays being normally disposed in three axes intersecting at right angles, and containing axial canals; elements either detached or fused together so as to form a lattice-like mesh. Dermal and flesh spicules exceedingly variable in form, but invariably six-rayed.

Next to the *Lithistida*, the *Hexactinellida* are the most abundant of the fossil silicious sponges. They are extraordinarily variable in form, and are often anchored by a tuft or "rope" of long, slender, glassy fibres, or are attached directly by the base. The walls are thin, as a rule, and enclose usually a wide cloaca; the canal-system is consequently much simpler than in the *Lithistida*, being made up merely of short tubes which penetrate the walls more or less deeply on both sides, and generally end blindly. Sometimes the sponge is entirely composed of thin-walled tubes which twine about one another irregularly and produce a system of lacunar interstices (intercanals) of greater or lesser size.

The skeletal elements proper are distinguished by their considerably larger size and uniform type of structure, from the usually minute, astonishingly variable and delicate flesh-spicules; the latter, unfortunately, are very seldom preserved in the fossil state. The skeletal elements occur detached in the soft parts in the *Lyssacina* group, or they are but partially or irregularly cemented together; in the *Dictyonina* group, on the other hand, the skeletal elements are regularly united in such manner that the rays of proximate elements are all closely applied against one another, and are surrounded by a continuous silicious envelope. In this way a more or less symmetrical lattice-work with cubical meshes is produced, in which, however, the fusion of juxtaposed elements is indicated by the fact that each ray contains two distinctly separated axial canals. The junction of the rays at the central node of each element is usually inflated, but is sometimes sculptured in such manner as to enclose a hollow octahedron (lantern nodes, lychnisks). The exterior of the skeleton is often covered by a dermal layer composed of irregular hexactins, in which the externally directed ray has become atrophied; or a dense silicious envelope is secreted, in which stellate hexactins with reduced outwardly and inwardly directed rays (stauractins) are embedded in greater or lesser profusion.

The *Hexactinellida* of the present day are distributed chiefly over the greater depths of the ocean beyond the hundred fathom line (200 to 3000 fathoms). They occur fossil principally in deep-sea deposits, and make their first appearance in the Cambrian; their period of greatest development falls in Jurassic and Cretaceous time.

Sub-Order A. LYSSACINA. Zittel.

Skeletal elements either entirely detached, or only partially and in an irregular fashion cemented together. Root-tuft often present.

The *Lyssacina* are poorly adapted for preservation in the fossil state, since the skeletal elements are but rarely cemented together to form a connected framework, and the flesh-spicules are invariably destroyed. Notwithstanding, complete sponges composed of large-sized, detached hexactins, have been found in Palaeozoic formations, and also in the Upper Jurassic of Streitberg; and, indeed, the oldest sponges that can be determined with certainty all belong to the *Lyssacina*.

Family 1. **Protospongidae**. Hinde.

Thin-walled, sac, tube-like, or spherical sponges, with walls composed of a single layer of cruciform tetraxial spicules (stauractins), so arranged as to form quadrate and subquadrate meshes. Elements non-fasciculate. The reticulation formed by the larger elements is divided into secondary squares by smaller spicules, so that the meshwork is constituted of several series of squares. Cambrian and Ordovician.

To this family belong the genera *Protospongia*, Salter, and *Phormosella*, Hinde.

Family 2. **Dictyospongidae**. Hall.

Usually large, funnel-shaped, cylindrical, or prismatic sponges, whose thin walls are frequently diversified by ridges and prominences. Skeletal framework very regular, and composed of larger and smaller quadrate meshes situated one within the other. Framework formed by bundles of slender spicules. Ordovician to Devonian. Chiefly in Devonian of North America and Europe.

Dictyophyton, *Uphantaenia*, Hall, and *Hydnoceras*, Conrad, occur usually in the form of well-preserved moulds in Devonian sandstones and slate; the silicious spicules are totally destroyed.

Family 3. **Plectospongidae**. Rauff.

Thin-walled tubes with skeleton composed of a regular framework made up of an ascending and approximately ring-like series of spicules; the latter form rectangular to quadrate, but not very symmetrical meshes. Spicular rays fasciculate. Ordovician and Silurian.

Cyathophycus, Walcott; *Palaeosaccus*, *Acanthodictya*, Hinde; Ordovician. *Plectoderma*, Hinde; Silurian.

Genera incertae sedis.

Pattersonia, Miller (*Strobilospongia*, Beecher). In form of large botryoidal clumps. *Brachiospongia*, Marsh. Vase-like sponges with broad inferior margin prolonged into a number of hollow arms; Ordovician of North America. These, together with *Amphispongia*, Salter, and *Astroconia*, Sollas, from the Silurian of England, represent extinct families of the *Lyssacina*.

Pyritonema, M'Coy (*Acestra*, Roem.) Fascicles of long, stout spicules, supposed to be root-tufts. Silurian.

Hyalostelia, Zitt. (*Acanthospongia*, Young). Skeletal elements relatively large, in the form of regular hexactins and stellate bodies with reduced vertical ray, and with inflated nodes. Root-tuft composed of elongated, slightly bent fibres, sometimes terminating in four recurved rays. Cambrian to Lower Carboniferous; Great Britain.

Holasterella, Carter, *Spiractinella* (Fig. 69), and *Acanthactinella*, Hinde, are allied genera occurring in the Carboniferous Limestone of Great Britain.

Tholiasterella, Hinde (Fig. 70), from the Carboniferous, has thin walls composed of a layer of robust, irregularly amalgamated hexactins. As a rule, two of the rays lying in the same plane divide dichotomously from the nodes outward, so as to produce a six-armed instead of a four-armed cross. In *Asteractinella*, Hinde (Fig. 71), all of the rays lying in the same plane divide in two or more branches, thus giving rise to many-rayed, extremely diverse, stellate, and corolla-like bodies. Carboniferous: Ayrshire.

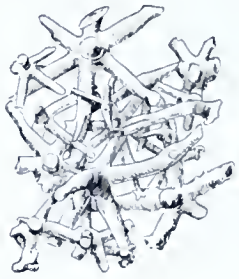

Fig. 70.

Tholiasterella gracilis, Hinde. Carboniferous Limestone; Dalry, Ayrshire. Dermal layer with fused stellate spicules, $^{5}/_{1}$ (after Hinde).

Astraeospongia Roem. (Fig. 72). Thick-walled, depressed, bowl-shaped, upper surface concave, lower convex, without traces of attachment. Skeleton composed of relatively large, homogeneous, uncemented cruciform spicules; six of the rays are disposed in the same plane, while the two rays projected at right angles to these are reduced to short, button-like prominences. Common in Silurian of Tennessee and Devonian of the Eifel.

Fig. 69.

Spiractinella Wrightii, Carter sp. Carboniferous Limestone; Sligo, Ireland. *A*, Normal hexactin. *B*, Hexactin with forked rays, $^{5}/_{1}$ (after Hinde).

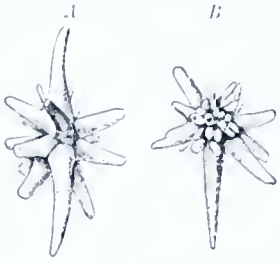

Fig. 71.

Asteractinella expansa, Hinde. Carboniferous Limestone; Dalry, Ayrshire. Skeletal element, $^{5}/_{1}$ (after Hinde).

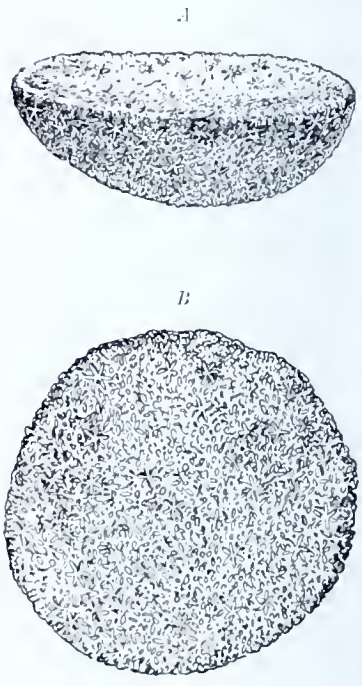

Fig. 72

Astraeospongia meniscus, Bumb. Silurian; Tennessee. *A*, Sponge, in profile, $^{2}/_{3}$ natural size. *B*, Upper surface of same.

According to Hinde, *Tholiasterella* and *Asteractinella* constitute a distinct order (*Heteractinellidae*), while *Astraeospongia* is made the type of the order *Octactinellidae*. I should prefer, however, to regard these two groups as aberrant Hexactinellids, in which supernumerary rays are produced by branching.

Sub-Order B. DICTYONINA. Zittel.

Skeletal spicules cemented to form a continuous framework in such a way that every arm of a hexactin is applied to the corresponding arm of an adjacent spicule, and both rays become enveloped in a common silicious covering. Root-tuft absent.

The *Dictyonina* are probably descendants of the *Lyssacina* (possibly from *Protospongia*- and *Dictyophyton*-like forms). They appear first in the Trias, and play a prominent *rôle* as rock-builders in the Jurassic and Cretaceous. Their lattice-like skeletons are frequently replaced by calcite, or are dissolved away

and merely indicated by cavities. The more important fossil forms are divided into the following families.

Family 1. **Craticularidae.** Rauff. (*Euretidae*, p. p., Zittel non Schulze.)

Cup-shaped, cylindrical, branching, or flattened sponges. Spicular nodes solid. External surface without distinct dermal layer, but protected by a thickening of the outer skeletal layer, and occasionally covered with a delicate web of cemented spicules. Canals simple, blindly terminating in the skeleton. Jurassic.

Tremadictyon, Zitt. (Fig. 73). Cup-, plate-shaped, or cylindrical, with wide cloaca. Canal-openings on both sides in alternating rows. Base nodular; exterior veiled over with delicate network of amalgamated hexactins, extending even across canal pores. Skeletal framework with more or less irregular cubical meshes. Very common in Upper Jurassic.

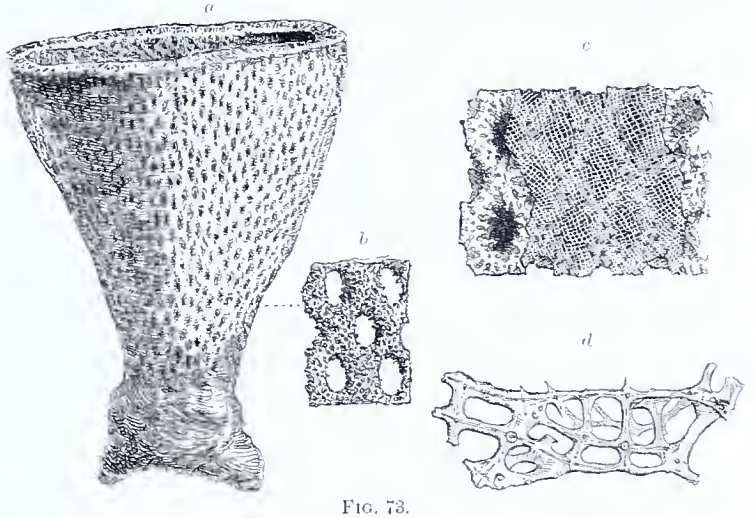

Fig. 73.

Tremadictyon reticulatum, Goldf. sp. Upper Jurassic; Streitberg, Franconia. *a*, Sponge, $^2/_5$ natural size; *b*, Enlarged portion of outer surface without dermal layer; *c*, Portion with well-preserved dermal layer. $^3/_1$; *d*, Skeleton, $^{12}/_1$.

Craticularia, Zitt. (Fig. 74). Funnel-shaped, cylindrical, or flattened; simple, or branching. Canal-openings on both surfaces either round or elliptical, and regularly distributed in vertical and horizontal rows. Canals short, ending blind. Jurassic, Cretaceous, and Miocene.

Sporadopyle, Zitt. Cup- to funnel-shaped or conical, occasionally branching. Canal-openings on outer surface irregularly distributed, or arranged in quincunx; on cloacal surface in vertical rows. Upper Jurassic. *S. obliqua*, Goldf. sp.

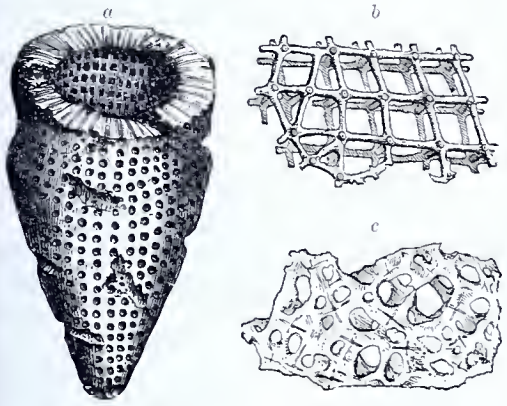

Fig. 74.

Craticularia paradoxa, Mnstr. sp. Upper Jurassic; Muggendorf, Franconia. *a*, Sponge, $^1/_3$ natural size; *b*, Latticed skeleton, $^{12}/_1$; *c*, Thickened dermal layer.

Sphenaulax, Zitt., *Verrucocoelia*, Etall, etc. Jurassic.

Family 2. **Coscinoporidae.** Zittel.

Calycoid, beaker-like, lobate, branching, or stellately convoluted sponges, with thin walls perforated on both sides by numerous canal-openings arranged in alternating

rows; canals short, ending blind. Framework compact, with fine meshes; dermal layer replaced by thickening of outermost skeletal layer. Spicular nodes solid, more rarely perforate. Cretaceous.

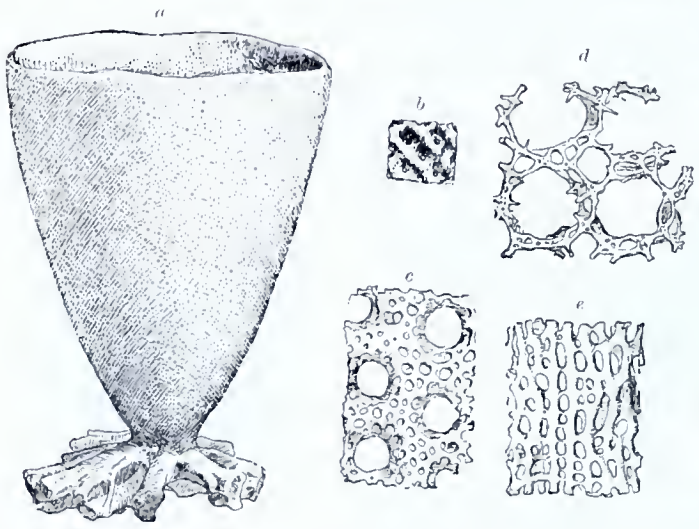

Fig. 75.

Coscinopora infundibuliformis, Goldf. Upper Cretaceous; Coesfeld, Westphalia. *a*, Complete individual, 1/2 natural size; *b*, Outer surface, natural size; *c*, Same, 3/1; *d*, Skeleton of cup, 12/1; *e*, Skeleton of root, 12/1.

Leptophragma, Zitt. Beaker-shaped, with root-like attachment. Walls thin, covered on both sides with small canal-openings arranged in alternating rows. Meshwork very closely woven, spicular nodes solid. Middle and Upper Cretaceous.

Pleurostoma, Roem., *Guettardia*, Mich. Cretaceous.

Coscinopora, Goldf. (Fig. 75). Beaker-like, with branching roots. Ostia small, round, and in alternating rows. Skeletal elements in part with perforated intersection nodes. Root consisting of long silicious fibres. Dermal layer formed by thickening and fusion of outermost hexactins. Cretaceous.

Family 3. Staurodermidae. Zittel.

Top-shaped, funnel-shaped, or cylindrical, more rarely branching or in clumps. Ostia and postica irregularly distributed, or in alternating rows. Skeletal framework more or less regular; intersection nodes thick or octahedrally excavated. The outer, or both surfaces of the wall provided with large, stellate spicules (stauractins), which differ from those of the rest of the skeleton, and are either but loosely cemented together, or are embedded in a continuous silicious skin. Jurassic and Cretaceous.

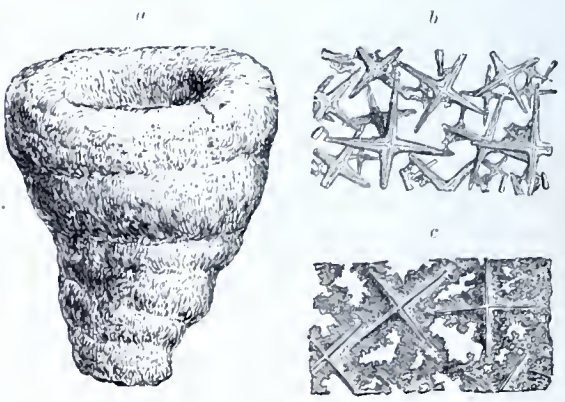

Fig. 76.

Cypellia rugosa, Goldf. sp. Upper Jurassic; Streitberg, Franconia. *a*, Sponge, 1/2 natural size; *b*, *c*, Dermal layer, 12/1.

Cypellia, Zitt. (Fig. 76). Top-shaped, bowl-shaped, or branching, without root. Canals irregularly distributed, crooked, and branched. Lattice skeleton with irregular meshes, intersection nodes perforated. Dermal layer composed of large, four-rayed stauractins embedded in a thin, continuous, or perforated skin. Very common in Upper Jurassic Spongitenkalk.

Stauroderma, Zitt. Funnel-shaped or plate-like, with broad and shallow cloaca, into which the large, round postica of short canals open. Inner and outer surfaces provided with dermal layer, in which stellate spicules are embedded with reduced externally and internally directed rays. Upper Jurassic.

Casearia, Quenst. Cylindrical, with numerous annular constrictions. Cloaca deep, tubiform; dermal layer relatively thick, and made up of cemented stellate spicules. Upper Jurassic. *C. articulata*, Goldf. sp.

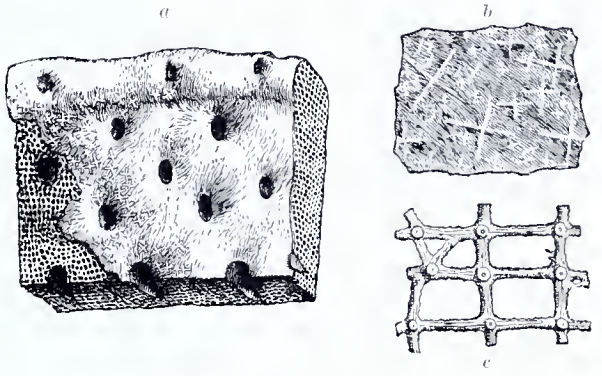

FIG. 77.

Porospongia impressa, Goldf. sp. Upper Jurassic; Muggendorf, Franconia. *a*, Fragment in natural size; *b*, Dermal layer, $^{6}/_{1}$; *c*, Skeleton, $^{12}/_{1}$.

Porospongia, d'Orb. (Fig. 77). Compressed and expanded, more rarely bulbous or cylindrical. Superior surface pitted with large exhalent apertures of short, blindly terminating cloacae, and covered over with a dense or finely perforate silicious skin, in which cruciform spicules and regular hexactins are embedded. Lattice skeleton with cubical meshes; intersection nodes imperforate. Upper Jurassic.

Family 4. **Ventriculitidae.** Toulmin Smith.

Wall intricately convoluted; folds radially disposed, generally vertical in direction. Radial canals ending blind. Longitudinal furrows developed along folds of the wall, and either open, or partially covered over with dermal layer, which is usually formed by thickening of the outer skeletal layer. Skeletal framework with octahedrally perforated nodes. Roots consisting of elongated silicious fibres united by transverse bridges and without axial canals. Jurassic and Cretaceous.

FIG. 78.

Pachyteichisma Carteri, Zitt. Upper Jurassic; Hohenpölz, Franconia. *a*, Sponge, $^{1}/_{2}$ natural size; *b*, Skeleton, $^{12}/_{1}$.

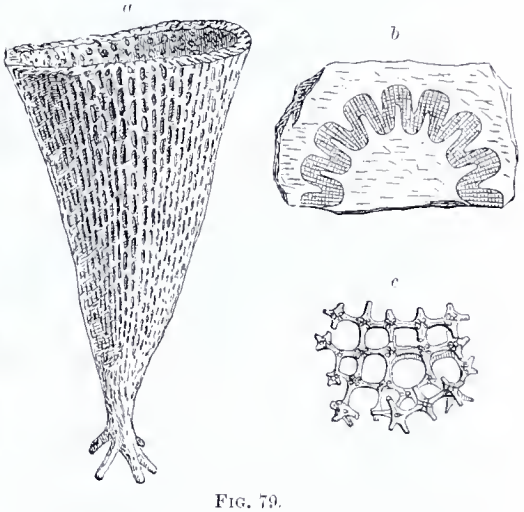

FIG. 79.

Ventriculites striatus, Smith. Quadratenkreide; Linden, near Hanover. *a*, Sponge, $^{1}/_{2}$ natural size; *b*, Transverse section, $^{1}/_{1}$; *c*, Skeleton, $^{12}/_{1}$.

Pachyteichisma, Zitt. (Fig. 78). Turbinate or bowl-shaped, with very thick,

convoluted wall. Folds separated on outer surface by deeply incised furrows, on inner surface by shallow furrows. Framework extremely regular. Root and dermal layer absent. Upper Jurassic.

Ventriculites, Mant. (Fig. 79). Bowl-, plate-, beaker-, funnel-shaped, or cylindrical, with wide cloaca. Wall thin, convoluted; folds separated on both sides by closely crowded longitudinal furrows. Lattice-work of skeleton more or less regular; outer layer thickened; roots present. Common in Middle and Upper Cretaceous.

Schizorhabdus, *Rhizopoterion*, *Polyblastidium*, Zitt.; *Sporadoscinia*, Pomel; *Lepidospongia*, Roem., etc. Cretaceous.

Family 5. **Coeloptychidae.** Zittel.

Umbel- or mushroom-shaped, with stalk. Wall thin, deeply folded. Convolutions radially arranged, becoming furcate toward periphery of umbel, and exposed on lower surface. Marginal and upper surface enveloped with porous dermal layer entirely covering the folds. Ostia only on under side of umbel, situated on backs of the folds. Framework: very regular; intersection nodes octahedral, perforated; rays of hexactins provided with slender, thorny processes.

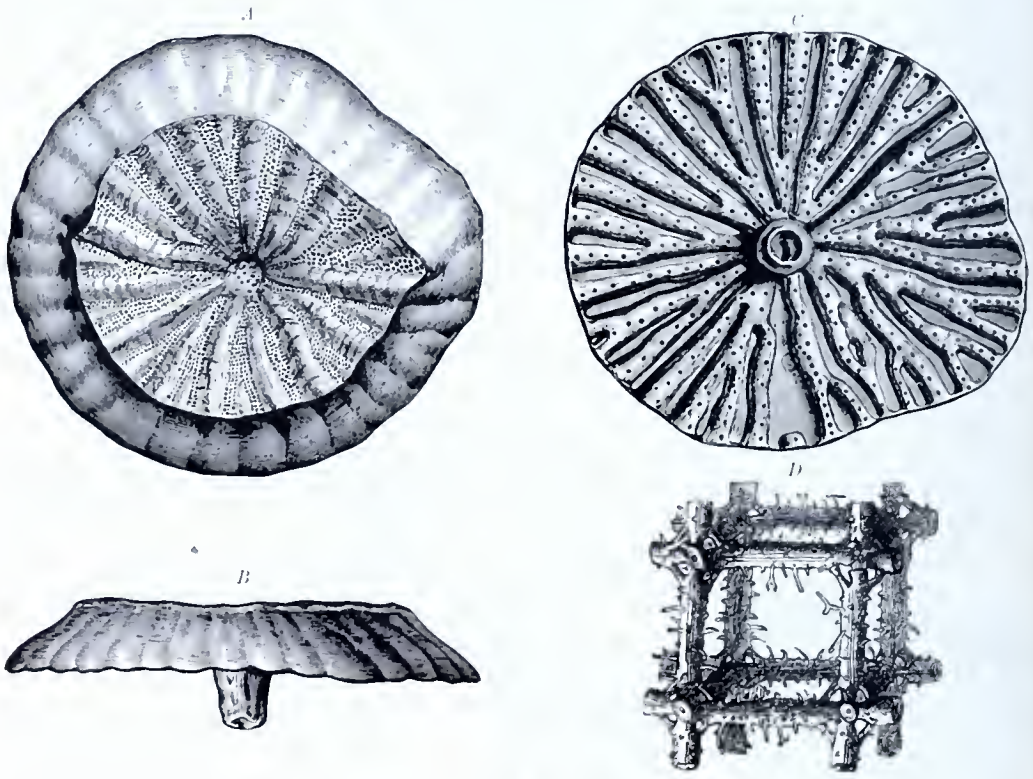

FIG. 80.

Coeloptychium agaricoides, Goldf. Upper Cretaceous; Vordorf, near Braunschweig. *A*, Top view. *B*, Profile. *C* Under surface, $^2/_3$ natural size. *D*, Skeleton, $^6/_1$

Coeloptychium, Goldf. (Fig. 80), occurring in the Upper Cretaceous of Northern Germany, England, and Southern Russia, is the solitary genus.

Family 6. **Maeandrospongidae.** Zittel.

Sponge body consisting of thin-walled, intricately labyrinthine, and partially amalgamated tubes or foliae, which form tuberous, pyriform, beaker-shaped, or bush-like branching stocks. Between the tubes are cavities and interstices of considerable size, which constitute the so-called intercanalicular system. Four canals faintly developed. Dermal layer absent, or represented by a continuous silicious superficial skin. Abundant in the Cretaceous, and also represented by numerous recent genera.

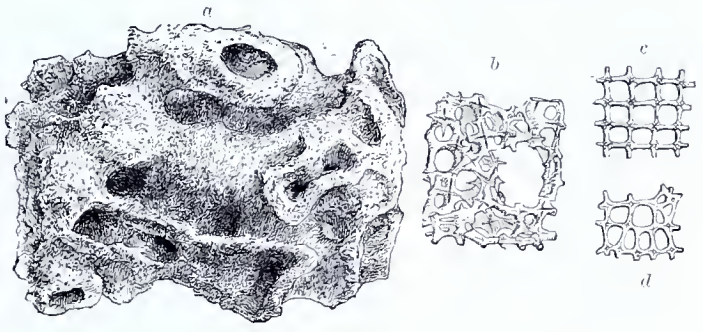

Fig. 81.

Plocoscyphia pertusa, Gein. Greensand (Cenomanian); Banowitz, Hungary. *a*, Fragment in natural size; *b*, Dermal layer, five times enlarged; *c*, Skeleton of interior, $^{12}/_{1}$; *d*, Outward portion of skeleton, $^{12}/_{1}$.

Plocoscyphia, Reuss. (Fig. 81). Clump-like or bulbous stocks consisting of labyrinthic, anastomosing tubes or foliae. Walls of tubes thin, perforated by numerous small ostia. Lattieed skeleton, interseetion nodes solid or perforate. Cretaceous.

Becksia, Schlüter (Fig. 82). The thin walls of the shallow, beaker-like sponge are composed of vertieal tubes having a radial disposition and fused with one another along the sides. Between the tubes are large interstices; near the base the tubes develop hollow, spinous processes. Lattiee skeleton very regular, exactly similar to *Coeloptychium*. Upper Cretaceous; Westphalia.

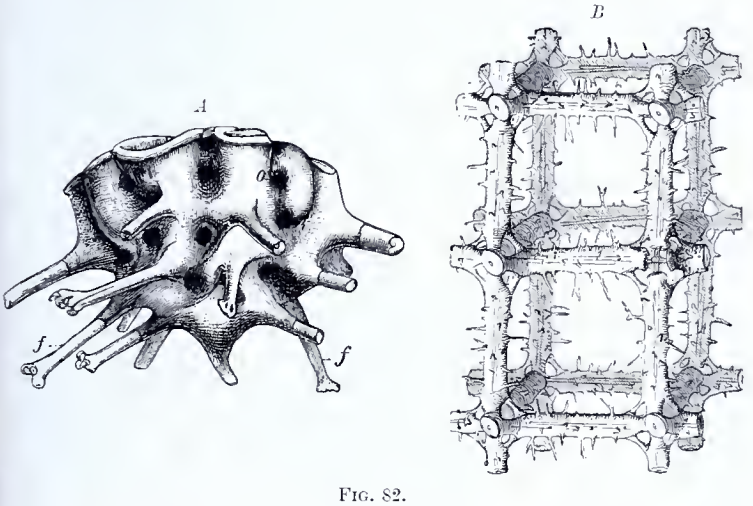

Fig. 82.

Becksia Sokelandi, Schlüt. Quadratenkreide; Coesfeld, Westphalia. *A*, Sponge body, $^{1}/_{2}$ natural size; *o*, Ostia of radial canals; *f*, Hollow, root-like processes of wall. *B*, Skeleton, $^{50}/_{1}$.

Tremabolites, Zitt.; *Etheridgia*, Tate; *Zittelispongia*, Sinzoff, etc. Upper Cretaceous.

Camerospongia, d'Orb. (Fig. 83). Globular, sub-globular, or pyriform. Upper half of the body enveloped by smooth silicious skin, and with large circular depression on the summit; lower half marked by undulating ridges and furrows, and passing gradually into a stem. Interior of sponge body consists of thin-walled, labyrinthous tubes. Upper Cretaceous.

Cystispongia, Roem. (Fig. 84). Like the preeeding, but with dense silicious

skin punctured by large, irregularly shaped apertures, uniformly enveloping the

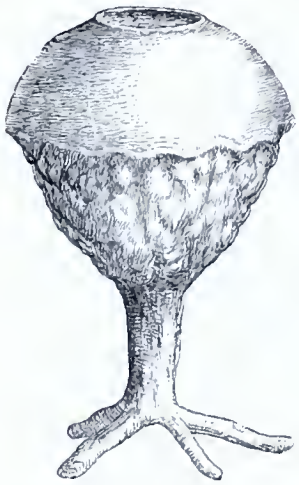

Fig. 83.

Camerospongia fungiformis, Goldf. sp. Planer; Oppeln, Silesia. Natural size.

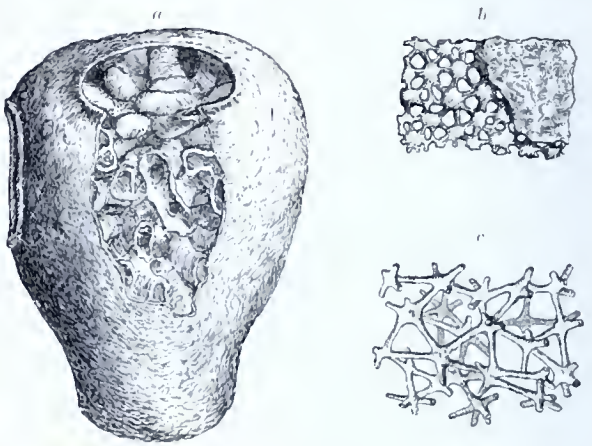

Fig. 84.

Cystispongia bursa, Quenst. Cuvieri-Planer (Turonian); Salzgitter, Hanover. *a*, Sponge, natural size; *b*, Dermal layer with underlying skeletal framework; *c*, Skeleton, $^{12}/_{1}$.

whole sponge body. Body composed entirely of tubes. Cretaceous and still living.

Sub-Class 4. **CALCISPONGIAE**. Calcareous Sponges.

Skeleton composed of calcareous spicules of three-rayed, four-rayed, or uniaxial types.

The external form of the Calcisponges is quite as variable as that of the silicious sponges, and reminds one particularly of the *Lithistida*. Like the Lithistids, too, the thick-walled *Leucones* and *Pharetrones* have a canal-system consisting of a central cavity into which radial excurrent canals conduct; while the numerous tributaries of the latter end in ciliated chambers which are fed by fine incurrent canals. In the *Sycones* the wall is perforated by simple radial tubes, but in the thin-walled *Ascones* it is pierced by mere holes.

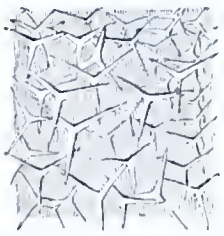

Fig. 85.

Triaxial skeletal elements of a recent *Ascon*, $^{50}/_{1}$.

The calcareous skeletal elements lie free in the soft parts, sometimes forming but a single layer disposed in the same plane (*Ascones*); sometimes their disposition is more or less distinctly radial, following the canal courses (*Sycones*); sometimes they are irregularly crowded together (*Leucones*); and sometimes they are closely apposed in the form of solid anastomosing fibres (*Pharetrones*). Regular triaxial spicules are of the most common occurrence, next monaxial spicules, sharpened on both sides, and more rarely four-rayed spicules.

Owing to the ready solubility of the skeletal elements in calcareous sponges, they are usually but poorly preserved in the fossil state, and are ill-adapted for microscopical investigation. The three-rayed and rod-shaped spicules which are united in fibres are seldom distinctly recognisable as such, since, as a rule, they are either wholly or partially dissolved, and are converted into homogeneous or crystalline fibres of calcite (Fig. 88); in these minute threads of calcite may be

seen radiating in all directions from numerous centres of crystallisation. Sometimes such calcareous skeletons afterwards become silicified. It is clear, therefore, that the present chemical composition of a fossil sponge furnishes us

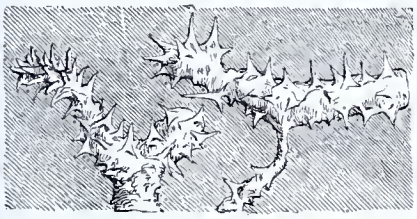

Fig. 86.

Fibres of a *Pharetrone*, composed of three-rayed spicules (*Peronidella cylindrica*, Goldf. sp. Upper Jurassic), $^{40}/_{1}$.

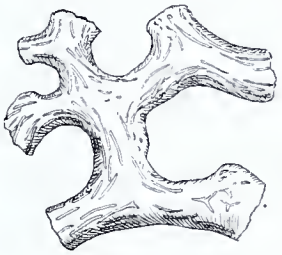

Fig. 87.

Solid fibres of fossil calcareous sponge with partially preserved spicules, $^{40}/_{1}$.

Fig. 88.

Fibres of fossil calcareous sponge altered by crystallisation, $^{40}/_{1}$.

no clue in regard to its original character, since during the process of fossilisation a silicious skeleton may become converted into a calcareous, and a calcareous into a silicious.

Of the four orders of calcareous sponges—*Pharetrones*, *Sycones*, *Ascones*, and *Leucones*—only the first two are of practical importance to the palaeontologist, traces of the others being either wanting or extremely fragmentary.

Order 1. PHARETRONES. Zittel.

Wall thick; canal-system like that of the Lithistida, though sometimes indistinct and apparently absent. Spicules arranged in solid anastomosing fibres; a smooth or corrugated dermal layer frequently present. Devonian to Cretaceous; unknown in Tertiary and Recent.

Eudea, Lamx. Cylindrical or club-shaped, usually simple, rarely branching. Cloaca narrow, tubiform, extending to the base, and terminating above in a

Fig. 89.

Peronidella cylindrica, Mnst. sp. Upper Jurassic; Muggendorf. Reduced $^{1}/_{2}$.

Fig. 90.

Peronidella dumosa, From. sp. Hils; Berklingen, Braunschweig. Natural size.

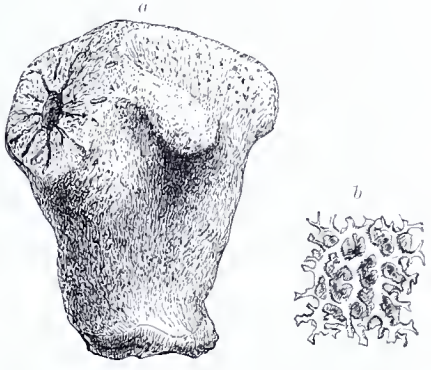

Fig. 91.

Corynella Quenstedti, Zitt. Coral-Rag; Nattheim. *a*, Sponge, natural size; *b*, Skeletal fibres, $^{4}/_{1}$.

round osculum. Dermal layer smooth, perforated by ostia of short canals. Triassic and Jurassic. *E. clavata*, Lamx.

Peronidella, Zitt. (antea *Peronella*, Zitt. non Gray, *Siphonocoelia*, *Polycoelia*,

From.), (Figs. 89, 90). Thick-walled, cylindrical, simple, or branching. Cloaca tubiform, extending to the base: base sometimes covered by dense dermal layer, the rest of the exterior finely perforate. A distinct canal-system absent. The coarse, anastomosing skeletal fibres composed of closely packed three-rayed and one-rayed spicules. Sparse in Devonian (*P. constricta*, Sandb. sp.); common in Trias, Jurassic, and Cretaceous.

Eusiphonella, Zitt. (Fig. 92). Similar to preceding, but thin-walled, with broad cloaca extending to the base, into which conduct radial canals arranged in vertical rows. External surface perforate. Upper Jurassic.

Corynella, Zitt. (Fig. 91). Knob-like, cylindrical, or top-shaped, thick-walled, simple, or composite. Cloaca funnel-shaped, shallow, terminating below in a series of vertical branching tubes; exhalent aperture often surrounded with radially diverging furrows. Ostia conducting into numerously branching radial canals, which unite again in larger excurrent canals, and open into the cloaca. Common in Trias, Jurassic, and Cretaceous.

Fig. 92.

Eusiphonella Bronni, Munst. sp. Coral-Rag; Nattheim. Natural size.

Fig. 93.

Oculospongia tubulifera, Goldf. sp. Kreidetuff; Maestricht. Natural size.

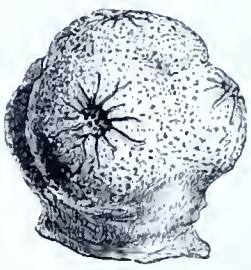

Fig. 94.

Stellispongia glomerata Quenst. sp. Coral-Rag; Nattheim. Natural size.

Stellispongia, d'Orb. (Fig. 94). Usually composite stocks made up of hemispherical, or short pear-shaped persons, with base enveloped by compact dermal layer. Summit dome-shaped, with shallow cloaca surrounded by radial furrows; radial and vertical canals terminating along sides and basis of cloaca. Skeleton constituted of short, blunt, and bent uniaxial, and also of three- and four-rayed spicules. Triassic and Jurassic.

Holcospongia, Hinde: Jurassic and Cretaceous. *Sestromostella*, Zitt.; Trias to Cretaceons. *Synopella*, Zitt.; Cretaceous. *Oculospongia* (Fig. 93) and *Diplostoma*, From.; Cretaceous.

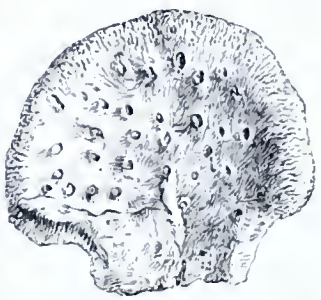

Fig. 95.

Elasmostoma acutimargo, Roem. Hils; Berklingen, Braunschweig. Upper surface, natural size.

Fig. 96.

Rhaphidonema Farringdonense, Sharpe sp. Lower Cretaceous (Aptian); Farringdon, Berkshire. ⅔ natural size.

Elasmostoma, From. (Fig. 95). Foliate-, ear-, or funnel-shaped. Upper (*i.e.* inner) surface covered with smooth dermal layer, in which large shallow oscula are situated; under surface cribriform. Cretaceons.

Rhaphidonema, Hinde (Fig. 96). Beaker-, funnel-, or twisted leaf-shaped. Inner or upper surface smooth, with very small oscula or pores. Outer surface rough, cribriform. Canal-system indistinct. Trias, Jurassic, Cretaceons.

Pachytylodia, Zitt. Funnel-shaped, thick-walled; base with smooth dermal

layer; oscula present here, but absent on other parts of exterior. Skeleton composed of very coarse, anastomosing fibres. Cretaceous. *P. infundibuliformis*, Goldf. sp.

Order 2. SYCONES. Haeckel.

Walls traversed by simple canals disposed radially with reference to the cloaca and opening into it. Skeletal elements very regularly arranged.

Mostly small, delicate forms inhabiting shallow water.

Protosycon, Zitt., from the Upper Jurassic of Streitberg, is a small, cylindrical, or conical form agreeing with living Sycons in the arrangement of its radial canals.

To the Sycons, also, Rauff assigns the calcareous sponge *Sphinctozoa* described by Steinmann (Jahrb. f. Mineralog. 1882, II. p. 139), which is distinguished from all other Calcisponges by having a most remarkable segmentation, such as occurs in the Lithistid genus *Casearia*.

The oldest Sycons are *Sollasia*, *Amblysiphonella*, and *Sebargasia*, Steinm., from the Carboniferous Limestone of Asturias. In the Triassic of St. Cassian and Seelandalp, near Schluderbach in Tyrol, are found *Colospongia*, Laube, *Thaumastocoelia*, and *Cryptocoelia*, Steinmann. *Thalamopora*, Roem., and *Barroisia*, Steinm., occur in the Lower and Middle Cretaceous.

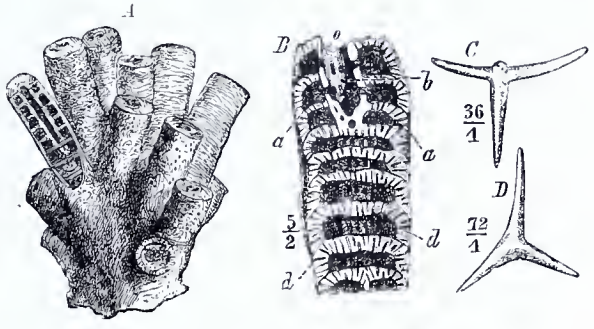

FIG. 97.

Barroisia anastomans, Mant. sp. Aptian; Farringdon, Berkshire. *A*, Bush-like colony, one person sliced open; natural size. *B*, Individual cut through obliquely, 5/2; *a*, Junction of two segments; *b*, Cloaca; *o*, Osculum; *d*, Radial canals. *C*, *D*, Three-rayed skeletal spicules, 36/1 and 72/1 (after Steinmann).

Barroisia (*Ventriculites*, Zitt. non Defr., *Sphaerocoelia*, Steinm.), (Fig. 97). Occurs sometimes as simple, cylindrical, or clavate individuals, and again in the form of bushy stocks. Outer surface frequently constricted, summit arched, with osculum in the centre, cloaca tubiform. The cylindrical individuals are composed of thin-walled, hemispherical, or compressed segments, which are so arranged that the roof of one segment serves also as the floor of the next following. The wall is everywhere perforated by simple radial canals, and is made up of fibres composed of three-rayed spicules. *B. helvetica*, Lor. sp. Aptian; La Presta, Switzerland.

Range and Distribution of Fossil Sponges.

The phylogeny of the *Myxospongiae*, *Ceratospongiae*, and a part of the *Silicispongiae*, owing to their perishable organisation, must ever remain involved in doubt. Nevertheless, isolated spicules prove the existence of Monactinellids and Tetractinellids in Palaeozoic seas; while in the Trias, Jurassic, and Cretaceous these forms become important rock-builders, and certainly play an active part in the formation of hornstone, chalcedony, and flint. In the Tertiary, spicules referable to existing genera are quite common.

The former distribution of the three best preserved sponge groups—the Lithistids, Hexactinellids, and Calcisponges—is noteworthy. The living representatives of the first two orders inhabit deep, or moderately deep water, while the calcareous sponges predominate in shallow waters bordering the coast. And hence, since fossil Calcisponges likewise occur almost entirely in marly, clayey, or sandy strata of undoubted littoral origin, and are absent in limestones where Lithistids and Hexactinellids predominate, it is plain that the distribution of both fossil and recent sponges has been occasioned by like physical conditions.

In the Cambrian occur the Lithistid genera *Archaeoscyphia* and *Nipterella*, and in the Ordovician and Silurian of Europe and North America are found a number of *Tetracladina* (*Aulocopium*) and *Eutaxicladina* forms (*Astylospongia*, *Palaeomanon*, *Hindia*), together with a few *Rhizomorina*. In the Carboniferous *Rhizomorina* and *Megamorina* are sparsely represented; but in the Upper Jurassic, and especially in the Spongitenkalk of Franconia, Swabia, Switzerland, and the Krakau district, the Lithistids exhibit an astonishing development, and occasionally form thick beds. They occur only sparingly in the Lower Cretaceous, but are abundant in the Pläner, Greensand, and Upper Cretaceous of Northern Germany, Bohemia, Poland, Galicia, Southern Russia, England, and France. The Tertiary being nearly everywhere made up of shallow-water formations, the absence of Lithistids and Hexactinellids is not surprising. They persist locally, however, as, for instance, in the Upper Miocene of Bologna, and in the Province of Oran in Northern Africa.

The range of the *Hexactinellida* is in every respect similar to that of the *Lithistida*. Beginning in the Upper Cambrian, they are represented in the Ordovician and Silurian by peculiarly modified *Lyssacina* forms (*Protospongia*, *Phormosella*, *Cyathophycus*, *Palaeosaccus*, *Plectoderma*, *Puttersonia*, *Brachiospongia*, *Dictyophyton*, *Astraeospongia*). The same group continues also through the Devonian, where *Dictyophyton* and its associates are conspicuous for their widespread distribution in North America. A few aberrant *Lyssacina*, which Hinde designates as *Heteractinellidae*, are found in the Carboniferous. During the Mesozoic and Cenozoic eras the distribution of the *Hexactinellida* is nearly identical with that of the *Lithistida*; although here and there beds occur which are charged principally with Hexactinellids, and others chiefly with Lithistids.

Very different conditions are presented by the Calcisponges, among which only the Pharetrones and Sycons are of geological importance. The oldest calcareous sponges occur very sparsely indeed in the Middle Devonian and Carboniferous Limestone. They appear in considerable diversity in the Alpine Trias (St. Cassian and Seelandalp), but outside the Alps are almost wholly absent. In the Jurassic they occur in marly beds of the Dogger (Ranville, Swabia), and also in certain facies of the Malm (Terrain à Chailles, Coral-Rag of Nattheim, Sontheim, etc.) in Southern Germany and Switzerland.

The Lower Cretaceous (particularly the Neocomian of Braunschweig, the Swiss Jura, and the Paris Basin), as well as the Aptian of La Presta, near Neuchâtel, and Farringdon, Berkshire; and also the Middle Cretaceous (Cenomanian) of Essen, Le Mans, and Havre, are characterised by an abundance of well-preserved Pharetrones, and a lesser number of Sphinctozooid Sycons. In the Tertiary, however, both groups are wanting, although the existence of

calcareous sponges is still indicated by occasional detached triactins. With the close of the Cretaceous, the Pharetrones seem entirely to have disappeared.[1]

Sub-Branch II. Cnidaria.

The *Cnidaria* or *Nematophora* have a radially symmetrical body, and a terminal mouth-opening surrounded by fleshy tentacles. In the ectoderm (sometimes also in the entoderm) enidoblasts are common, from the contents of which thread-cells (*nematocysts*), filled with an urticating fluid and containing a hollow, spirally coiled thread, are developed. Each cnidoblast possesses a fine superficial process (*cnidocil*), which is very sensitive to mechanical stimuli. The mesoderm is sometimes entirely absent, but the ectoderm and entoderm are strongly developed. The ectoderm or mesoderm frequently secretes a calcareous or horny skeleton, and both ectoderm and entoderm are concerned in the production of muscles and nerves. The sexual organs are the product of the entoderm.

The *Cnidaria* are divided into two classes: *Anthozoa* and *Hydrozoa*.

Class 1. ANTHOZOA = ACTINOZOA. Coral Polyps.[2]

Usually sessile, cylindrical polyps, possessing a mouth surrounded by tentacles, oesophagus, and gastrovascular cavity. The latter is divided by numerous vertical partitions (mesenteric folds) into a system of radially disposed pouches. A calcareous or horny skeleton is frequently developed.

The simple polyp individuals have the form of a cylindrical or conical tube, at the distal end of which is situated a muscular disk perforated centrally by the slit-like or oval fissure of the mouth. The mouth is furnished with a ring of tentacles round its margin, and opens into a membranous oesophageal tube

[1] To the sponges, and in fact to the Hexactinellids, Hinde has referred the singular group *Receptaculidae* occurring in the Ordovician, Silurian, and Devonian Systems. These are all free, globular, cup-, or platter-shaped bodies containing a central cavity, and whose calcareous wall is composed of elements arranged in quincunxial order. The elements lying on the outer or under side of the wall consist of small rhomboidal plates having four transverse rays disposed cross-wise, and one inwardly directed vertical ray. The systematic position of these problematical fossils (*Receptaculites, Leptopoterion, Pascolus, Ischadites, Polygonosphaerites*) is wholly conjectural; Gümbel assigns them to the calcareous algae (*Dactyloporidae*), and others to the Foraminifera or Sponges. *Vide* monograph by *Rauff* in Abhandlungen k. bayer. Akademie, II. Cl., Bd. XVII., 1892.

[2] *Milne-Edwards, H.*, et *Haime, J.*, Histoire Naturelle des Corallaires: 3 vols. and atlas. Paris, 1857-60.

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conducting into the gastric cavity. The outer covering of the body, whose parts are designated as wall, oral disk, and pedal disk, are constituted of ectoderm and entoderm, between which is a thin layer of mesoderm (*Mesogloea*). Six, eight, or more radially disposed vertical partitions (*mesenteries*), (Figs. 98, 99), projecting inwardly from the body-wall, divide the gastric cavity into a series of radiating compartments (*mesenteric pouches*). The mesenteries are prolonged upwardly as the hollow, muscular tentacles; while the generative organs are attached to their faces near the lower end of the body. The mesenteries are covered on both sides with muscular tissues, and bear mesenteric filaments on their curled inner edges. On one side of the mesenteries the muscle fibres are transversely directed, on the other longitudinally. The longitudinal system is usually considerably folded and thickened; and the disposition of these muscular portions (*Muskelfahne*) is of great importance from a systematic standpoint, since it reveals the bilateral symmetry of many Anthozoans, and enables one readily to identify the antimeres. If a polyp individual be cut in two by a plane passing through the longer axis of the mouth-opening, then, in the *Octocoralla* (Fig. 98), the mesenteries of the right half will have all the muscular thickenings disposed on the right-hand side, and those of the left on the left-hand side. In the *Hexacoralla* (Fig. 99) the mesenteries are grouped in pairs, with the muscular thickenings of any pair facing each other. Two pairs, however (those corresponding with the opposite extremities of the longitudinal mouth), form often an exception to this rule, since these have the muscular thickenings placed on opposite sides. These are called the *directive mesenteries*, and serve to indicate the longitudinal axis of the body.

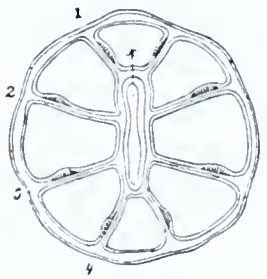


Fig. 98.

Diagrammatic section of the soft parts of an *Octocoralla* (*Alcyonium*). *s*, Oesophagus; 1, 2, 3, 4, Mesenteries of the left side (after R. Hertwig).

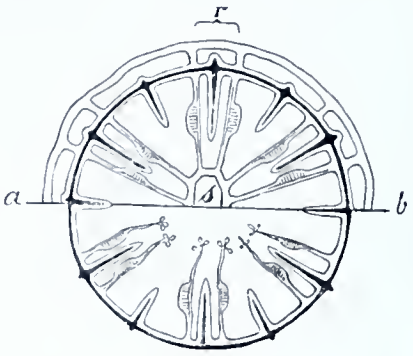


Fig. 99.

Diagrammatic section of the soft parts of a *Hexacoralla*. In the upper half (above the line *a—b*) the section passes through oesophagus *s*; in lower half, beneath the same. Corallum indicated by heavy lines. *r*, directive mesenteries.

Only a few *Anthozoa* have permanently soft bodies; the majority secreting calcareous, horny, or partly horny and partly calcareous structures, termed the skeleton or corallum. The simplest form of corallum is that composed of microscopic, round, cylindrical, acerate, or tuberculated spicules of carbonate of lime, which are developed in great quantities in the mesoderm and remain detached in the soft parts (many *Alcyonaria*). In a number of forms (*Corallium*, *Mopsea*, *Tubipora*) the spicules are firmly cemented together by means of a calcareous or horny connective substance, in such a manner as to form tubes (*Tubipora*), or, when the secretion takes place chiefly at the base, a sclerobase, or axis. Surrounding the axis is the soft *coenosarc* in which the polyps of the colony are embedded (Fig. 100). In some cases the sclerobase is composed entirely of horny matter without admixture of calcareous secretions. In the so-called "stone corals" (Fig. 101) a consistent calcareous skeleton is formed by the outer surface of the ectoderm. At the base of the polyp between each

pair of mesenteries, the infolded ectoderm secretes small, round, oval, or irregular calcareous bodies (*sclerites*); these are opposed against one another in radial directions, and as others are successively laid down on the top of them, upright partitions or *septa* (*Sternleisten*, *cloisons*) are built up. Gradually, also, as the polyp approaches maturity, the basal plate becomes calcified, owing to the secretion by the outer surface of the ectoderm of numerous minute, closely crowded, calcareous bodies. The septa, however, grow considerably above the base, and become lodged in the vertical interspaces between the mesenteries. In the same manner, within the soft body-wall, a calcareous secretion may take place, binding the outer edges of the septa together, and known as the *wall* or *theca* (*Mauer*, *Wand*, *muraille*). Both septa and theca are composed of minute, densely crowded calcareous bodies, in which delicate calcareous fibres may be seen radiating in all directions from a central dark space. And since

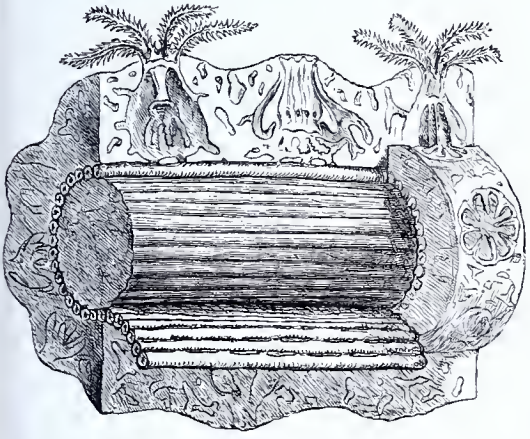


FIG. 100.

Corallium rubrum, Lam. (after Lacaze-Duthiers). Branch of red coral of commerce laid open along the axis, and showing three polyps in section embedded in fleshy coenosark.

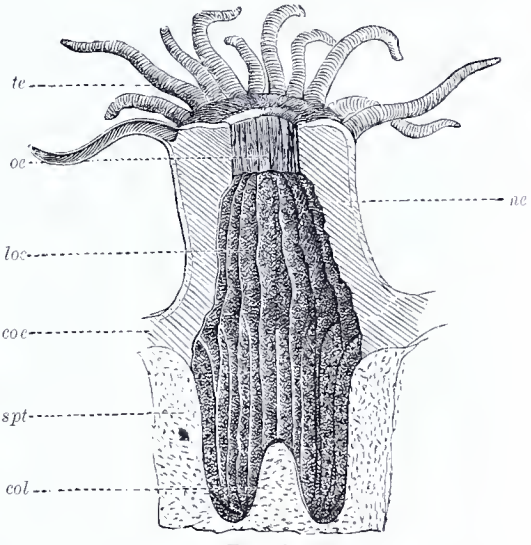


FIG. 101.

Astroides calycularis, Lamx. sp. Mediterranean (after Lacaze-Duthiers). Enlarged longitudinal section of polyp with calcareous skeleton. *te*, Tentacles; *oe*, Oesophagus; *me*, Mesentery; *loc*, Mesenterial pouches; *coe*, Coenosark; *spt*, Septum; *col*, Columella.

all the calcareous bodies forming the septa have a radial disposition, the calcification-centres as seen in transverse sections form a dark, mostly interrupted, and occasionally jagged median line, from which bundles of minute fibres radiate outward in all directions. Similar calcification-centres are found also in the theca. Sometimes the median dark line is uninterrupted and divides the septum into two separate lamellae.

The interstices between the sclerites forming the septa are either completely filled with carbonate of lime (*Aporosa*), or there remain larger or smaller porous spaces (*Perforata*); in many cases, in fact, the septa are represented by a loose network of sclerites piled up vertically, or merely by vertically directed spines.

The number of mesenteries and septa within the visceral chamber is equal to that of the tentacles, and is somewhat uniform throughout the different sub-classes, orders, genera, and species. Increase takes place, as a rule, in such a manner that whenever, as the polyp grows, a new visceral chamber is formed,

a new septum is secreted. The number, width, thickness, and mode of formation of the septa furnish important systematic characters, usually four, six, eight, or twelve principal or primary septa are first formed, between which septa of the second, third, and fourth cycles and so on are successively intercalated. The upper edges of the septa are sometimes smooth, sometimes serrated or granulated; and they extend from the central depression to the walls of the theca, either obliquely or in a curved line. This open, central depression, formed by the superior edges of the septa, is known as the *calice* (*Kelch*, *calyx*).

The sides of the septa are rarely smooth, but are commonly granulated or furnished with rows of small prominences; occasionally they are provided with well-marked vertical cross-bars (*carinae*). When the projections on the sides of the septa are in the form of conical or cylindrical transverse bars, they are termed *synapticula*. Frequently the synapticula of two adjacent septa become joined together; sometimes whole rows of them are fused together to form perpendicular bars, thus greatly strengthening the septal framework. In some corals (*Athecalia*) the development of synapticula is such as to render an outer wall superfluous. With the upward growth of the polyp, the theca gradually becomes elevated, and its lower portions, as their occupation by the soft parts ceases, are partitioned off by numerous horizontal or oblique calcareous plates which bridge over the interseptal spaces. These structures are known as *dissepiments* (*Traversen*) and *tabulae* (*Böden*); the tabulae are often nothing but highly developed dissepiments, being distinguished from the latter merely by the fact that they extend across between the septa at the same level; sometimes they are perfectly horizontal, sometimes they are arched or funnel-shaped (Fig. 102), and sometimes incomplete. Dissepiments and tabulae are most strongly developed in cylindrical forms, and frequently fill the included space within the theca with a vesicular or cellular tissue.

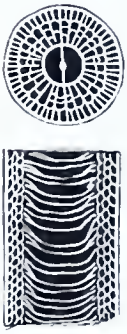


Fig. 102.

Lithostrotion Martini, E. and H. Longitudinal section showing tabulae.

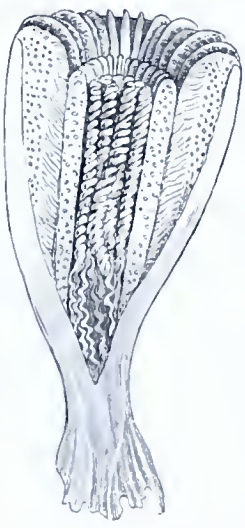


Fig. 103.

Cyathophyllia cyathus, Sol. Corallum split open longitudinally; true columella in the centre, surrounded by a cycle of pali.

When a number or when all of the septa are produced as far as the centre of the calice, their free edges may become twisted so as to form an axial structure, known as a *pseudo-columella*. Sometimes, however, a true columella (*Saulchen*, *Axe*) is present; this may be either a compact, styliform, or foliaceous structure, or may be composed of a bundle of styliform or twisted rods (Fig. 103), or of thin lamellae. It extends from the floor of the visceral chamber to the bottom of the calice, into which it projects for a greater or less distance. The structures known as *pali* (*Pfählchen*, *paluli*) are narrow vertical plates which are inserted between the columella and the inner ends of the septa in one or more cycles (Fig. 103).

The outer wall or *theca* is often formed by the secretion of a particular ring-like fold of the ectoderm, and is constituted of distinct sclerites, having separate calcification-centres, and connecting the outer edges of the septa

(*Euthecalia*). In many cases the peripheral edges of the septa become thickened and laterally fused to form a spurious theca (*Pseudothecalia*); and occasionally the dissepiments lying in a certain zone become united so as to form an inner wall within the true theca. The *epitheca* is a usually smooth, sometimes corrugated, superficial calcareous investment, which, according to Koch, is merely a prolongation of the basal plate, and is secreted by the outer surface of the ectoderm, which is reflected over the top of the corallum. The epitheca is deposited either directly upon the theca, or, when the septa are produced outwards so as to form exothecal lamellae or ribs (*costae*), the theca and epitheca are separated. Exothecal lamellae, not corresponding in position to the septa, are called *pseudocostae* or *rugae*.

Sexual reproduction is comparatively rare among Anthozoans. Following fertilisation and segmentation of the ova, ciliated larvae are born, which swim about for a time, become fixed, and develop into simple polyp individuals. Asexual reproduction by gemmation or fission is much more common. The individuals produced in this way remain connected with one another and with the parent animal, forming polyp stocks or colonies of exceedingly various forms and sizes.

New corallites are produced either within or without the calice of the parent polyp. In *extra-calicinal gemmation*, the buds are thrown out either from the sides of the polyp (*lateral gemmation*), or are formed in the common calcareous matrix which unites the various corallites of a colony (*coenenchymal* and *costal gemmation*). In both cases the new corallites may diverge from one another, being attached to the parent corallum only at the base, or they may grow up closely opposed to the latter and to one another, so that the thecae are in contact on all sides. In this way, branched, dendroid, or massive and knob-like ("astraeiform") compound coralla are formed. A less common mode of increase is by *basal* or *stolonal gemmation*. In this process the wall of the original polyp sends out creeping prolongations (stolons) or basal expansions, out of which new corallites arise. In *calicinal gemmation* buds are produced within the calice of the parent corallite, according to one or the other of the following methods:—Either certain particular septa become enlarged and produced so as finally to enclose a new calicinal disk (*septal gemmation*); or tabulae are produced upwards in the form of pockets, from which new corallites are developed (*tabular gemmation*). In both septal and tabular gemmation, a portion of the parent corallite including a part of the original wall is concerned in the formation of buds; while the septa or modified tabulae are converted into portions of the new thecae, from which new septa then begin to grow inwards toward the centre.

A peculiar kind of calicinal gemmation is that known as *rejuvenescence*. In this method only one bud is formed within the parent calice, but it enlarges until it completely fills the latter. By the indefinite repetition of this process, a corallum is formed, consisting of a succession of cups placed one within the other, of which only the youngest and uppermost is occupied by the living animal.

The beginning of reproduction by *fission* is marked by an elongation or distortion of the parent calice, accompanied by the contraction of the wall at opposite points along the margin. The constriction may proceed until it divides the oral disk into two halves; or two opposite septa may unite to form a new theca. By this method, branching, massive, or astraeiform colonies are produced, which do not differ essentially from those formed by budding.

Frequently, however, individuals formed by fission become only imperfectly separated, remaining proximally more or less closely in contact. In such cases the calices form continuous, straight, curved, or labyrinthic furrows, with more or less clearly distinguishable centres.

The compound corallum of a polyp stock remains practically the same as in solitary individuals, excepting that the conditions are more complicated when the separation of the individuals is incomplete. Dendroid and astraeiform colonies frequently develop a common connective matrix or tissue (*coenenchyma*) which unites the various corallites into a whole; it is secreted externally to the theca by an inverted external part of the polyp over the top of the corallum (*Randplatte*), and is sometimes dense in structure (*Oculinidae*), or it may consist of a vesicular or tubular tissue. The separate corallites are often also united by means of the septa, which are produced over and beyond the thecae, and fused with those of neighbouring individuals. In such cases the interseptal loculi are almost always filled with strongly developed dissepiments. All structures developed in the included space within the theca, with the exception of the septa, are designated collectively as *endotheca*: those lying without the theca as *exotheca*.

The *Anthozoa* are exclusively marine forms, and predominate in shallow water. Many of the *Actiniaria*, *Antipatharia*, and *Madreporaria* occur also at greater depths, ranging from 50-300, and sometimes even to 1500 fathoms. The so-called *reef-corals* inhabit depths not exceeding 30-35 metres, and require a temperature of the water of about 18° to 20° C. Hence, existing coral-reefs are restricted to a zone extending about 30° on either side of the equator; they are distinguished according to form as fringing reefs, barrier reefs, and atolls. While the stony corals (*Porites*, *Madrepora*, *Turbinaria*, *Pocillopora*, numerous *Astraeidae* and *Fungidae*) and the Alcyonarians (*Heliopora*) are the most important, they are not the only agents concerned in the formation of reefs, as an active part is also played by the *Hydromedusae* (*Milleporidae*), calcareous algae (*Lithothamnium*, *Melobesia*), mollusks, echinoderms, bryozoans, and worms. Of the ancient coral-reefs which have been formed in nearly all of the great geological periods, those of the Cenozoic and Mesozoic periods are composed in part of genera similar to those now living; while those of the Palaeozoic represent genera and families that are now principally extinct, and whose relation to living forms is often quite uncertain.

The *Anthozoa* are divided by Haeckel into three sub-classes—*Tetracoralla*, *Hexacoralla*, and *Octocoralla*.

Sub-Class 1. TETRACORALLA. Haeckel.[1]

(*Zoantharia Rugosa*, Milne-Edwards; *Pterocorallia*, Frech.)

Extinct, palaeozoic, simple, or composite sclerodermic corals, with septa arranged according to a tetrameral system, and either bilaterally or radially symmetrical;

[1] Literature (cf. also p. 67):

Kunth, A., Beiträge zur Kenntniss fossiler Korallen. Zeitschrift der deutschen geologischen Gesellschaft, Bd. XXI., 1869, and XXII., 1870.

Dybowski, W. N., Monographie der Zoantharia Rugosa, etc. Archiv für Naturkunde Liv-, Est-, und Kurlands, Bd. V., 1874.

Roemer, F., Lethaea Palaeozoica, 1883, pp. 324-416.

Schlüter, Clem., Anthozoen des rheinischen Mittel-Devons. Abhandlungen der preussischen geologischen Landes-Anstalt, Bd. VIII., 1889.

without coenenchyma, but with usually strongly developed endothecal tissue in the form of tabulae or dissepiments, and with well-marked, frequently wrinkled wall.

The *Tetracoralla* are especially characterised by the possession of four principal or primary septa, between which four sets of new septa are subsequently developed. The four principal septa are sometimes of equal proportions, when they may be either stouter and longer than the others (*Stauria*), or thinner and shorter (*Omphyma*); or they may be of unequal proportions. Of the two principal septa which lie in the longitudinal axis of the corallum, one (called the *cardinal septum*) is frequently situated in a depression or furrow known as the *fossula* (Fig. 104); while the other or *counter septum* is either normally developed, or is more or less reduced. Occasionally the counter septum is placed in a fossula, while the cardinal septum is normally developed; but the two laterally disposed or *alar septa* are always equal in size. The remaining septa not infrequently exhibit a well-marked radial arrangement, in which the longer and more strongly developed usually alternate with the shorter and less strongly developed. New septa, according to Kunth and Dybowski, are inserted in the following order. First, a new septum is given off on either side of the cardinal septum (Fig. 104, *h*), and takes up a position parallel with the alar septum. This leaves an intermediate space between the cardinal and the newly formed septa, which becomes filled, however, by the repeated insertion of new septa one above the other in the same manner as the first; and hence they diverge from the cardinal septum, as they grow upward, in a pinnate fashion. Likewise the two counter quadrants lying between the alar and counter septa become occupied by lamellae which are given off from the alar septa, and gradually arrange themselves parallel with the counter septum. The mode of growth in the *Tetracoralla* will be readily understood on inspecting the surface of such specimens whose septa are visible on the exterior, or whose wall is readily removed by corrosion or polishing. One may then note three distinct lines extending from the calicinal margin to the base; these mark the cardinal and the two alar septa, from which the other pinnately branching septa are directed obliquely upward (Fig. 105). The order in which the septa are given off in the four quadrants is indicated by the numerals in Fig. 104.

Fig. 104.

Menophyllum tenuimarginatum, E. and H. Carboniferous Limestone; Tournay, Belgium. 2/1. *h*, Cardinal septum; *g*, Counter septum; *s*, Alar septa.

Fig. 105.

Zaphrentis Canadensis, Bill. Ordovician; Cincinnati, Ohio. Natural size.

Many of the *Tetracoralla* multiply by sexual reproduction, and occur only as single individuals; asexual reproduction takes place usually by calicinal, more rarely by lateral gemmation, and results in dendroid or massive colonies.

Dissepiments are generally abundantly developed between the septa, which latter are compact, and the upper edges of which are either smooth or serrated. Sometimes the dissepiments fill the whole interior with a vesicular tissue, and the central visceral cavity is frequently entirely partitioned off by horizontal, inclined, or funnel-shaped tabulae. The wall is usually composed

of the thickened and fused septal edges; sometimes it is invested with epitheca and furnished with vertical rugae or root-like processes. A true coenenchyma is absent. In a few genera the calice is provided with a lid or opercular, which may be composed of one (*Calceola*) or of several plates (*Goniophyllum*).

With the exception of a few genera whose systematic position is uncertain, all the typical *Tetracoralla* are confined to the Palaeozoic rocks. They are probably the ancestors of the imperforate *Hexacoralla*.

Family 1. **Cyathaxonidae.** Milne-Edwards and Haime.

Turbinate or horn-shaped coralla, occurring only simple. Septa with regular radial arrangement. Tabulae and dissepiments absent.

Fig. 106.

Cyathaxonia cornu, Mich. Carboniferous Limestone; Tournay. Corallum with fractured theca, showing open interseptal loculi. $^2/_1$.

Fig. 107

Petraia radiata, Must. Devonian; Enkeberg, near Brilon. $^1/_1$. *a*, Corallum viewed from the apex; *b*, Transverse section below the middle.

Fig. 108.

Polycoelia profunda, Germ. sp. Zechstein; Gera. $^1/_1$ (after Roemer).

Cyathaxonia, Mich. (Fig. 106). Acutely pointed, conical. Cardinal septum in fossula. Septa numerous, extending inward as far as the strongly developed styliform and considerably elevated columella. Carboniferous Limestone; Belgium and England.

Duncanella, Nich. Corallum top-shaped. Septa nearly all of uniform length and size, forming a spurious columella in centre of the deep calice, exsert at the base. Silurian; North America. *D. borealis*, Nich.

Petraia, Münst. (Fig. 107). Turbinate or conical. Septa short, reaching to the centre only at the base of the very deep calice. Columella absent. Ordovician to Carboniferous.

Polycoelia, King. (Fig. 108). Horn-shaped. Calice very deep; four principal septa reach nearly to its centre, between which in each quadrant are five shorter septa. Zechstein.

Kunophyllum, Dyb. Ordovician and Silurian.

Family 2. **Palaeocyclidae.** Dybowski.

Corallum simple, discoidal, or bowl-shaped. Septa numerous, stout, approaching radial symmetry in disposition. Tabulae and dissepiments wanting.

Palaeocyclus, E. and H. (Fig. 109). Discoidal to depressed top-shaped, with epitheca. Septa numerous, radially disposed, the larger ones reaching to the centre. Silurian.

Combophyllum, *Baryphyllum*, E. and H. Devonian.

Fig. 109.

Palaeocyclus porpita, Lin. Silurian; Gottland. *a*, Top view of calice; *b*, Profile. $^1/_1$.

Fig. 110.

Microcyclus discus, Meek and Worth. Hamilton (Devonian); North America. $^1/_1$. *a*, Corallum from below; *b*, from above (after Nicholson).

Hadrophyllum, E. and H. Cushion-shaped, with epitheca. Calice with three septal fossula, that of the cardinal septum being the largest. Devonian; Eifel and North America.

Microcyclus, Meek and Worth. (Fig. 110). Like the preceding, but with only one septal fossula. Devonian; North America.

Family 3. **Zaphrentidae.** Milne-Edwards and Haime.

Coralla simple, turbinate, conical, or cylindrical; septa numerous, exhibiting distinct bilateral symmetry in arrangement. Theca generally formed by fusion of septal ends. Tabulae completely developed; dissepiments not very abundant in interseptal loculi.

Streptelasma, Hall. Turbinate, often curved. Septa numerous (80-130), alternately long and short; the free edges of the longer septa are twisted together in the centre to form a pseudocolumella. Tabulae few or absent. Position of the principal septum is recognisable on the exterior by system of pinnately diverging costal ridges. Common in Ordovician and Silurian.

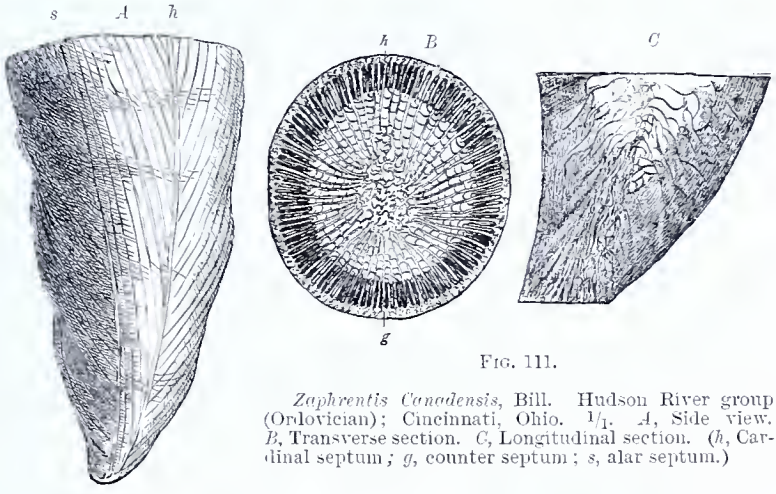


FIG. 111.

Zaphrentis Canadensis, Bill. Hudson River group (Ordovician); Cincinnati, Ohio. 1/1. *A*, Side view. *B*, Transverse section. *C*, Longitudinal section. (*h*, Cardinal septum; *g*, counter septum; *s*, alar septum.)

Zaphrentis, Raf. (Figs. 111-114). Simple, turbinate, or sub-cylindrical, frequently elongated. Calice deep, with circular margin. Septa numerous, reaching to the centre; cardinal septum in a deep fossula. Tabulae numerous, somewhat irregular, and passing from side to side of the visceral chamber;

FIG. 112.

Zaphrentis cornicula, Lesueur. Devonian limestone; Ohio.

FIG. 113.

Zaphrentis cornucopiae, Mich. Calice enlarged. Carboniferous Limestone; Tournay, Belgium.

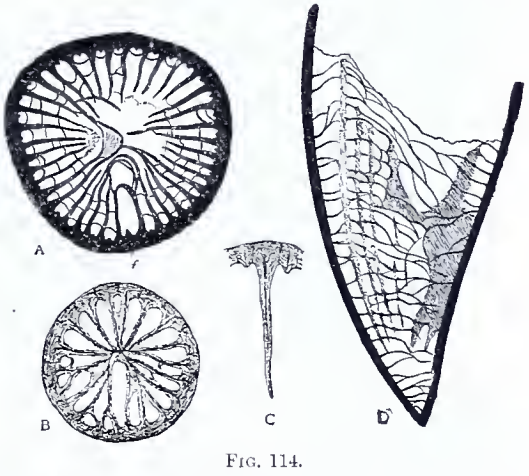


FIG. 114.

Zaphrentis Enniskilleni, Nich. Carboniferous Limestone; Ireland. *A*, *B*, Transverse sections through respectively upper and lower portions of calice. *C*, A long and two short septa united at the ends to form the wall. *D*, Longitudinal section showing tabulae (after Nicholson).

dissepiments sparingly developed in outer zone of corallum. 50-60 species known, ranging from Silurian to Carboniferous. Maximum development in Carboniferous.

Amplexus, Sow. Simple, sub-cylindrical, or elongated turbinate. Calice shallow, usually with septal fossulae. Septa moderately numerous, short, never produced to centre. Tabulae highly developed, horizontal. Ordovician to Carboniferous limestone.

Aulacophyllum, E. and H. Turbinate. Septa numerous, extending to centre. Cardinal septum in deep fossula; adjacent septa pinnately developed. Ordovician to Devonian.

Menophyllum, E. and H. (Fig. 104). Turbinate. Cardinal septum in largest of three fossula. Carboniferous limestone.

Lophophyllum, E. and H. Carboniferous limestone. *Anisophyllum*, E. and H. Ordovician to Devonian. *Pycnophyllum*, Lindstr. Ordovician and Silurian. *Apasmophyllum*, Roem. *Metriophyllum*, E. and H. *Thamnophyllum*, Penecke. Devonian. *Pentaphyllum*, de Koninek. Carboniferous.

Family 4. **Cyathophyllidae.** Milne-Edwards and Haime.

Simple or composite coralla. Septa numerous, radially arranged; the four principal septa rarely distinguished by greater or smaller size. Tabulae and vesicular tissue (dissepiments) abundant.

Cyathophyllum, Goldf. (Figs. 115-117). Extremely variable in form, sometimes simple, turbinate, or sub-cylindrical; sometimes giving rise to

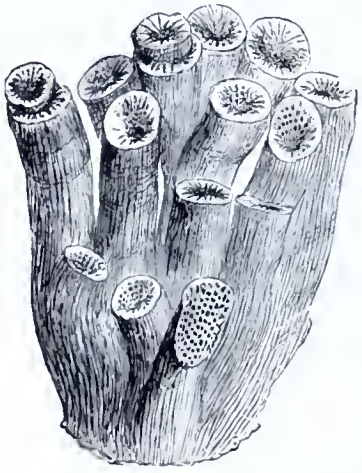


Fig. 115.

Cyathophyllum caespitosum, Goldf. Devonian; Gerolstein, Eifel. Natural size.

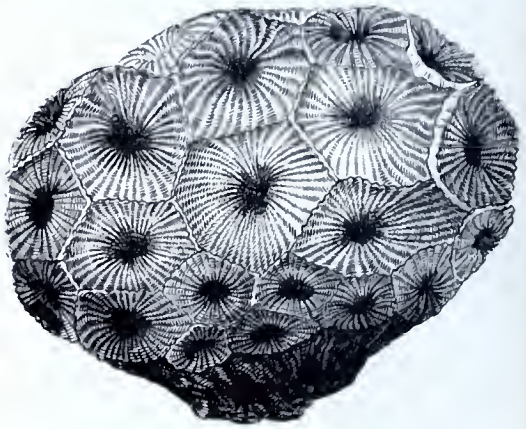


Fig. 116.

Cyathophyllum hexagonum, Goldf. Devonian; Gerolstein, Eifel. Natural size.

bushy, fasciculate, or astraeiform colonies, where reproduction takes place by calicinal or lateral gemmation. Septa very numerous, strictly radial in arrangement, and often alternately long and short; the longer septa extending to the centre. Visceral chamber filled with numerous imperfectly developed tabulae; vesicular dissepiments highly developed in peripheral portion. Nearly 100 species known, ranging from Ordovician to Carboniferous limestone. Maximum development in Devonian.

Campophyllum, E. and H. (Fig. 118). Like the preceding, but septa not extending to the centre. Devonian and Carboniferous Limestone.

Heliophyllum, Hall. Usually simple and turbinate, more rarely forming

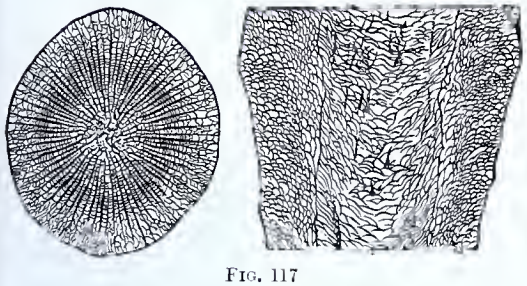


Fig. 117

Cyathophyllum heterophyllum E. and H. Middle Devonian; Gerolstein, Eifel. *A*, Transverse; *B*, Longitudinal section (after Nicholson).

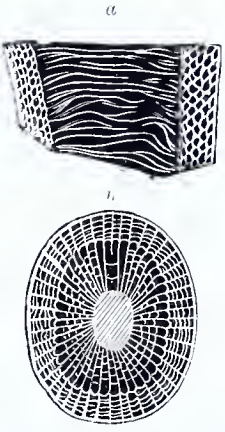


Fig. 118.

Campophyllum compressum, Ludw. Carboniferous Limestone; Hausdorf, Silesia. *a*, Longitudinal; *b*, Transverse section.

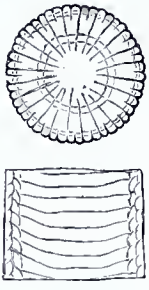


Fig. 119.

Diphyphyllum concinnum, Lonsd. Carboniferous Limestone; Kamensk, Ural.

dendroid colonies. Septa numerous, extending to the centre, and thickened on their sides by conspicuous vertical ridges ("carinae"). Devonian.

Diphyphyllum, Lonsd. (Fig. 119). Ordovician to Carboniferous. *Pholidophyllum*, Lindstr. Ordovician and Silurian. *Eridophyllum*, E. and H. Silurian

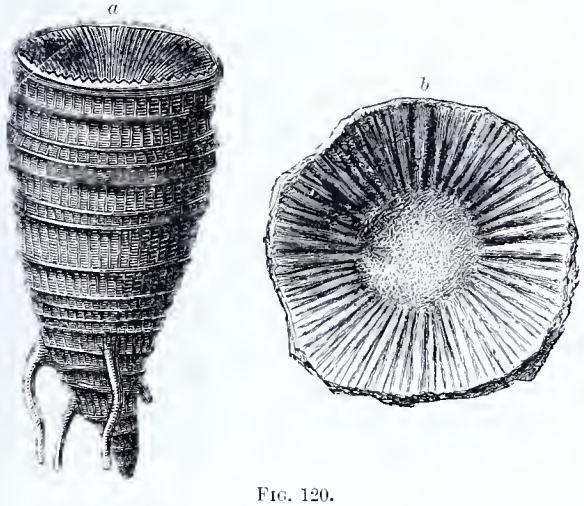


Fig. 120.

Omphyma subturbinata, E. and H. Silurian limestone; Gottland, Sweden. *a*, Side view; *b*, Calice from above.

Fig. 121.

Lithostrotion Martini, E. and H. Carbon. Limest.; Hausdorf, Silesia. Sections of individual corallite (after Kunth).

and Devonian. *Crepidophyllum*, Nich. *Craspedophyllum*, Dyb. Devonian. *Koninckophyllum*, Nich. *Chonaxis*, E. and H. Carboniferous. *Clisiophyllum*, Dana. Silurian to Carboniferous.

Omphyma, Raf. (Fig. 120). Corallum simple, conical, or turbinate; theca with root-like processes. Septa numerous; the four principal septa in shallow

fossula. Surface marked with pinnately branching striae. Tabulae numerous. Silurian.

Chonophyllum, E. and H. Silurian and Devonian.

Ptychophyllum, E. and H. Simple and turbinate, or composite. Each stock is composed of funnel-shaped, invaginated layers, representing calicinal buds, the marginal lips of which are more or less reflected outwards. Septa numerous and strongly twisted in the centre to form a pseudo-columella; their peripheral edges are thickened and are fused with one another so as to form a wall. Silurian (*P. patellatum*, Schlot. sp.) and Devonian.

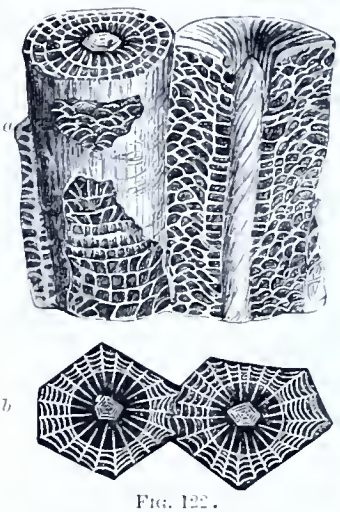


FIG. 122.

Lonsdaleia floriformis, Lonsd. Carboniferous Limestone; Kildare, Ireland. 1/1. *a*, Two cylindrical corallites, partially split open; *b*, Two hexagonal calices, seen from above.

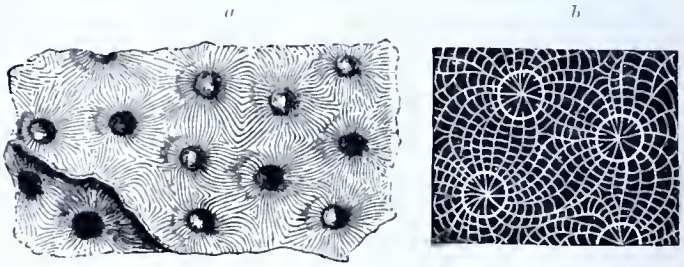


FIG. 123.

Phillipsastraea Hennahi, E. and H. Devonian limestone; Ebersdorf, Silesia. *a*, Upper surface; *b*, Transverse section. Natural size.

Cyclophyllum, Duncan and Thom. Simple, cylindro-conical. Septa numerous, the longer ones forming a thick pseudo-columella with enclosed spongy tissue.

Aulophyllum, E. and H., *Aspidophyllum*, *Rhodophyllum*, Nich. and Thoms., etc. Carboniferous.

Lithostrotion, Llwyd. (*Stylaxis*, M'Coy; *Petalaxis*, E. and H.), (Fig. 121). Fasciculate or astraciform stocks composed of prismatic or cylindrical corallites.

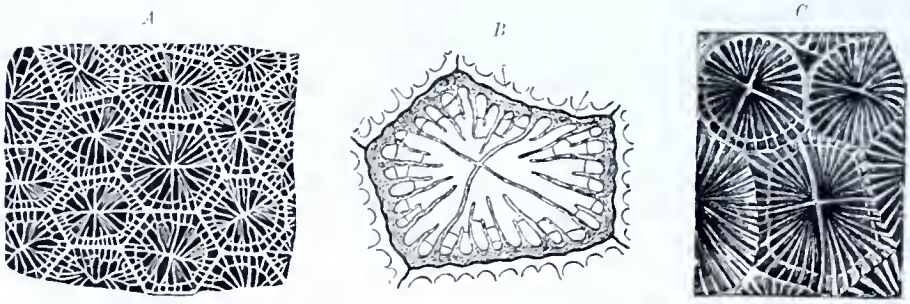


FIG. 124.

Stauria astraeiformis, E. and H. Silurian; Gottland, Sweden. *A*, Transverse section parallel to upper surface. *B*, Enlarged transverse section of individual corallite. *C*, Several calices from above. Natural size (after Nicholson).

Septa numerous, alternately long and short. Styliform columella in the centre. Abundant in Carboniferous limestone.

Lonsdaleia, M'Coy (Fig. 122). Fasciculate or astraeiform, composite coralla. Septa well developed; columella large, composed of vertically rolled lamellae. Central tabulate area bounded by an interior dissepimental wall,

between which and the theca vesicular endotheca is abundantly developed. Common in Carboniferous rocks.

Strombodes, Schweigg. Astraeiform stocks composed of small prismatic corallites. Septa extremely numerous, very slender, extending to the centre. Theca imperfectly developed. Visceral chamber filled with infundibuliform tabulae and vesicular tissue. Silurian (*S. typus*, M'Coy sp.) and Devonian.

Pachyphyllum, *Spongophyllum*, E. and H. Silurian and Devonian.

Acervularia, Schweigg. Astraeiform or bushy colonies. Septa stout and numerous. An interior wall is present; tabulae are developed in the central area, while the peripheral zone is filled with vesicular tissue. Silurian (*A. ananas*, Lin. sp.) and Devonian.

Phillipsastraea, E. and H. (Fig. 123). Astraciform colonies, with individual corallites united by confluent septa, which are produced beyond the theca, and obscure the same. Interseptal loculi filled with vesicular endotheca. Devonian and Carboniferous.

Stauria, E. and H. (Fig. 124). Astraeiform or bushy composite coralla. Septa well developed; the four principal septa characterised by larger size, and forming a complete cross in centre of each corallite. Silurian (Wenlock).

Columnaria, Goldf. (*Favistella*, Hall). Astraciform stocks, composed of long, polygonal, thick-walled corallites. Septa radially arranged in two cycles, alternately long and short, barely reaching the centre. Tabulae horizontal, disposed at regular intervals apart, and stretching across the entire visceral chamber. Dissepiments imperfectly developed or absent. Ordovician to Devonian.

Heterophyllia, M'Coy. Carboniferous. *Battersbyia*, E. and H. Devonian.

Family 5. **Cystiphyllidae.** Milne-Edwards and Haime.

Usually simple coralla. Septa very thin; interseptal loculi filled with vesicular endotheca or compact stereoplasma. Tabulae absent; central area of visceral chamber either completely filled with vesicular tissue or stereoplasma, or containing the same only in the lower portions of chamber. Calcareous operculum sometimes present.

Cystiphyllum, Lonsd. (Figs. 125, 126). Simple, very rarely forming bushy colonies. Calice deep; the entire visceral chamber filled with vesicular tissue, which, as a rule, wholly obliterates the numerous lineally directed septa. Silurian and Devonian.

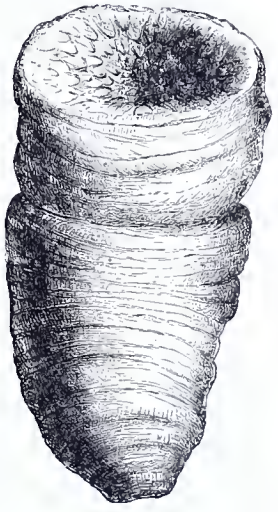


Fig. 125.

Cystiphyllum vesiculosum, Goldf. Devonian; Eifel. Natural size.

Strephodes, M'Coy (Fig. 127). Usually simple coralla. Septa well developed, alternately long and short, sometimes forming a pseudo-columella. Silurian to Carboniferous.

Goniophyllum, E. and H. (Fig. 128). Corallum simple, in the form of a four-sided pyramid, and covered with thick epithecal deposit. Calice deep; septa numerous, thick and very short. Entire visceral chamber filled with vesicular and stereoplasmic endotheca. Operculum composed of four plates symmetrically paired. Silurian.

Rhizophyllum, Lindst. Corallum simple, pyramidal, or hemispherical,

flattened on one side; external surface corrugated, and sending off hollow, root-like exothecal processes. Calice marked with septal striae; internal

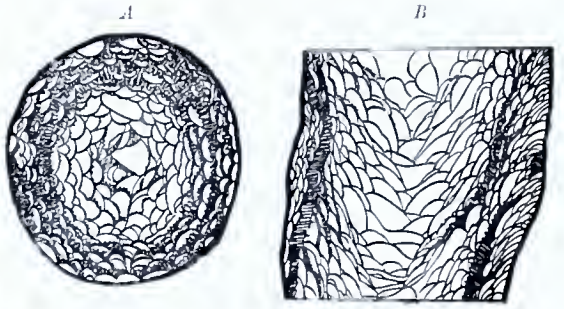


Fig. 126.

Cystiphyllum cylindricum, Lonsd. Silurian; Iron Bridge, England. *A*, *B*, Transverse and longitudinal sections (after Nicholson).

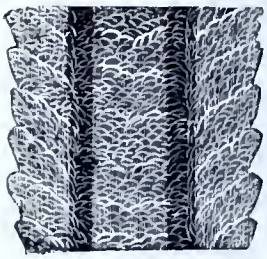


Fig. 127.

Strephodes Murchisoni, Lons. Showing strongly developed dissepiments and tabulae.

structure consisting of vesicular tissue and stereoplasma. Operculum in form of semicircular plate; inner surface traversed by median ridge and fainter, granulated, parallel elevations. Silurian.

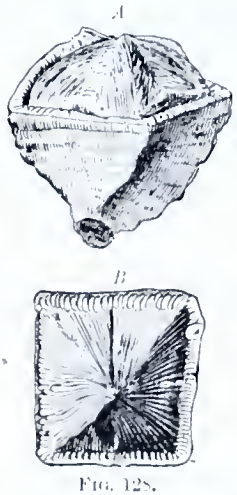


Fig. 128.

Goniophyllum pyramidale, His. sp. Silurian; Gottland. *A*, Specimen with operculum. *B*, Calice seen from above. Natural size (after Lindstrom).

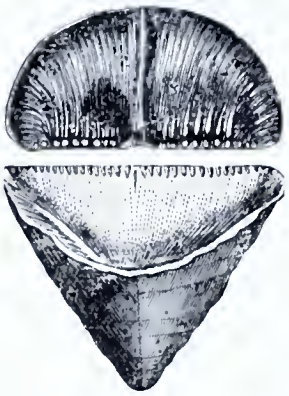


Fig. 129.

Calceola sandalina, Lam. Devonian; Eifel. Natural size.

Calceola, Lam. (Fig. 129). Corallum simple, semi-turbinate, or slipper-shaped, with one side flat and triangular. Calice very deep, extending nearly to apex, and marked internally with fine septal striae. Cardinal septum placed in the centre of the vaulted side, counter septum in middle of flattened side, and alar septa at the angles. Internal structure composed of fine vesicular tissue and stereoplasma. Operculum semicircular, very thick, under surface marked with prominent median and fainter lateral septal ridges. *C. sandalina*, Lam. Very common in Middle Devonian of Europe, rare in Carboniferous Limestone of Belgium.

Range and Distribution of the Tetracoralla.

The typical Tetracoralla are confined to the Palaeozoic rocks. They are unknown in the Cambrian, and make their first appearance in the Ordovician, where they are sparsely represented in North America and in Europe. Here the most abundantly distributed genus is *Streptelasma*; *Cyathophyllum* and *Ptychophyllum* being of rarer occurrence. The period of maximum development falls in the Silurian, which contains the largest number of genera and species. There are limestones found on the islands of Gottland and Dago (Esthonia), as well as at Dudley, Shropshire, and at Lockport, New York, and other places in North America, which are made up of ancient coral-reefs. The principal agents

concerned in the formation of these reefs were *Cyathophyllum*, *Heliophyllum*, *Omphyma*, *Ptychophyllum*, *Strombodes*, *Acervularia*, *Stauria*, *Aulacophyllum*, *Cystiphyllum*, etc., of the *Tetracoralla*, besides numerous *Tabulata*, *Octocoralla*, *Bryozoa*, and Echinoderms. The *Tetracoralla* are not less conspicuous in the Devonian, especially in the Middle and Upper Devonian of the Eifel district, Westphalia, Nassau, Harz, Boulogne, England, and North America. Particularly abundant here are the genera *Cyathophyllum*, *Combophyllum*, *Zaphrentis*, *Cystiphyllum*, *Phillipsastraea*, *Calceola*, etc. *Zaphrentis*, *Amplexus*, *Lithostrotion*, *Lonsdaleia*, *Cyclophyllum*, etc., predominate in the Carboniferous Limestone of Belgium, England, Ireland, and North America; while in the Zechstein the solitary genus known is *Polycoelia*. On the other hand, the Permo-Carboniferous rocks of the Salt Range in Farther India and of the island Timor contain the genera *Zaphrentis*, *Amplexus*, *Clisiophyllum*, and *Lonsdaleia*. According to Frech, the genera *Gigantostylis*, *Pinacophyllum*, and *Coccophyllum*, occurring in the Alpine Trias, belong to the *Tetracoralla*; and to this group also have been assigned *Holocystis*, E. and H., from the Cretaceous, and the recent genera *Haplophyllum*, Pourtalès, and *Guynia*, Duncan. A number of Palaeozoic *Tetracoralla*, such as *Battersbyia*, *Heterophyllia*, and *Stauria*, are referred by Duncan and Nicholson to the *Hexacoralla* (*Astraeidae*).

Sub-Class 2. HEXACORALLA. Haeckel.

(*Zoantharia*, Blainville; *Hexactinia* and *Polyactinia*, Ehrenberg.)

Simple or composite polyps, with radial mesenteries arising in cycles of six, twelve, or multiples of six; frequently with calcareous corallum, but sometimes fleshy or with horny axis.

To the *Hexacoralla* belong the calcareous reef-building and deep-sea corals (*Madreporaria*) of the present day, the fleshy sea-anemones (*Actiniaria*), and those forms characterised by the secretion of a horny axis (*Antipatharia*). Of these three orders, only the *Madreporaria* are known in a fossil state. These forms are distinguished from the *Tetracoralla* by the hexameral system and radial arrangement of mesenteries and septa; and from the *Octocoralla*, in addition to the above-named characters, by their simple tentacles. In the *Madreporaria*, six, or more rarely twelve principal septa spring from the base of the theca, and between these new septa originate in such manner that all similarly situated mesenteries become simultaneously provided with an additional septum. The corallum, accordingly, consists of at least six, but usually of a larger number of septa, whose disposition is strictly radial. The six principal septa form the first cycle, and at the

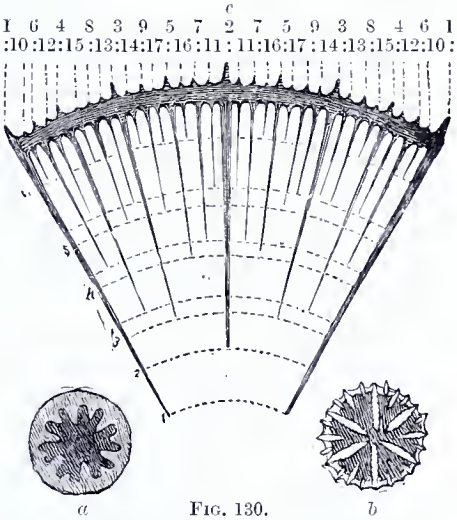


Fig. 130.

Diagram illustrating Milne-Edwards and Haime's law of septal growth in the *Hexacoralla*. *a*, Young corallum with two cycles of septa; *b*, Corallum with three cycles of septa; *c*, Segment of calice with six cycles of septa. (The numerals above Fig. *c* indicate the order of insertion of new septa. The concentric dotted lines mark the beginning and end of the several cycles; the figures on the left indicate the order of cycles, and are placed opposite the line touched by the last septum of a given cycle.)

same time mark off the boundaries between which new cycles of successively six, twelve, twenty-four septa, etc., are inserted. The septa of any cycle are usually all of about the same length and thickness, those of the later cycles being almost invariably of lesser proportions than those of the earlier. This law of septal growth, however, which was first accurately determined by Milne-Edwards and Haime (Fig. 130), is by no means strictly adhered to. Irregularities in the growth of new septa may result in a penta-, hepta-, or octameral arrangement. Reproduction takes place either sexually, when separate individuals are produced; or asexually, by means of lateral or basal gemmation; or by fission. In composite coralla, the individual corallites are sometimes united by a common coenenchyma. Endothecal structures are frequently present in the form of synapticula, dissepiments, and tabulae.

The order of stone corals or *Madreporaria* (*Zoantharia sclerodermata*) was divided by Milne-Edwards and Haime into five sub-orders: *Rugosa*, *Tabulata*, *Tubulosa*, *Perforata*, and *Aporosa*. Of these, the *Rugosa* have been elevated by Haeckel into a separate sub-class under the name of *Tetracoralla*. The groups *Aporosa* and *Perforata* are called *Hexacoralla*; while the affinities of the *Tabulata* (with which the *Tubulosa* are now generally included) are still unsatisfactorily determined. The group is certainly composed of a varied assemblage of forms, some of which have been assigned to the *Hexacoralla*, some to the *Octocoralla*, and some to the *Hydrozoa* and *Bryozoa*.

[Miss Ogilvie, D.Sc., will shortly publish a work on the "Structure and Classification of Corals," in which the subdivisions of the *Madreporaria* into *Tetracoralla* and *Hexacoralla* are entirely abandoned, on the ground that the *tetrameral* septal system is merely an ancestral feature strongly marked in certain of the older families, while *hexameral* septal symmetry is but one of many forms of radial symmetry (pentameral, octameral, decameral, dodecameral, etc.), developed in the course of time within this group of corals. The further subdivision of *Hexacoralla* into *Aporosa* and *Perforata* is also discontinued by Miss Ogilvie, who classifies the whole of the *Madreporaria* ("stone corals") into a number of families of equal rank. These are:—*Zaphrentidae*, *Cyathophyllidae*, *Amphiastraeidae* (a new family of Palaeozoic—Recent age, including *Stauria*, *Columnaria*, *Pinacophyllum*, *Amphiastraea*, *Aplosmilia*, *Euphyllia*, etc.), *Turbinolidae* (including the *Cyathaxonidae* and *Trochosmilinae*), *Oculinidae*, *Pocilloporidae* (including the *Stylophorinae* with the genera *Astrocoenia* and *Stephanocoenia*), *Madreporidae* (including the *Turbinarinae*), *Stylinidae*, *Astraeidae* (excluding the *Eusmilinae*, Edw. and H.), *Fungidae* (including the *Thamnastraeinae*), *Eupsammidae* (including the *Stylophyllinae*, *Epistreptaphyllum*, *Diplaraea*, etc.), *Archaeocyathidae*, and *Poritidae*.—THE AUTHOR.]

Order 1. MADREPORARIA. Milne-Edwards.

Radially symmetrical sclerodermous corals with typically hexameral (rarely pentameral, heptameral, or octameral) arrangement of septa.

Sub-Order A. APOROSA. Milne-Edwards and Haime.

Septa and theca compact; interseptal loculi usually partitioned off by dissepiments or synaptioles, more rarely by tabulae, seldom empty throughout. Theca either independently secreted, or formed by fusion of the septal edges, or absent.

Family 1. **Turbinolidae.** Milne-Edwards and Haime.

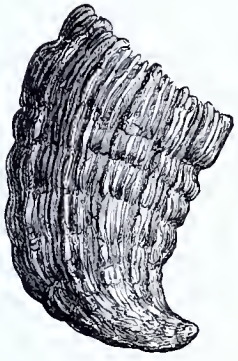
Corallum simple, very seldom composite; septa numerous, long, and with entire margins. Interseptal loculi empty throughout. Columella usually, pali often present. Theca complete.

The *Turbinolidae* begin in the Jurassic, and are especially abundant in the Tertiary and at the present day. Sexual reproduction prevails, although a few forms multiply by gemmation; the buds, however, become separated from the parent animal at an early period.

Turbinolia, Lam. (Fig. 131). Corallum free, conical, with circular calice. Septa produced outside the theca. Styliform columella present. Tertiary and Recent; common in Calcaire Grossier of the Paris Basin, and Eocene of England.

Fig. 131.

Turbinolia Bowerbanki, E. and H. Eocene; Highgate, England. $^6/_1$.



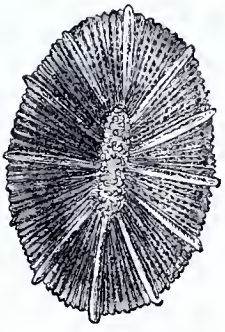


Fig. 132.

Ceratotrochus duodecimocostatus, Goldf. sp. Miocene; Baden, near Vienna. Natural size.

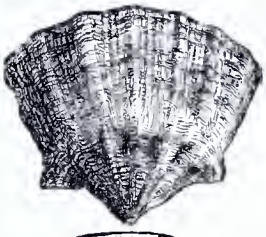


Fig. 133.

Flabellum Roissyanum, E. and H. Miocene; Baden, near Vienna. Natural size.

Sphenotrochus, E. and H. Free, cuneiform, with elongated calice; columella foliaceous. Cretaceous to Recent. *S. crispus*, Lam. Common in Calcaire Grossier of the Paris Basin.

Smilotrochus, E. and H.; *Stylotrochus*, From.; *Onchotrochus*, Duncan. Cretaceous; *Discotrochus*, E. and H. Tertiary, etc.

Ceratotrochus, E. and H. (Fig. 132). Horn-shaped; young forms attached at the apex. Septa very numerous, produced above the theca; columella fasciculate. Cretaceous to Recent.

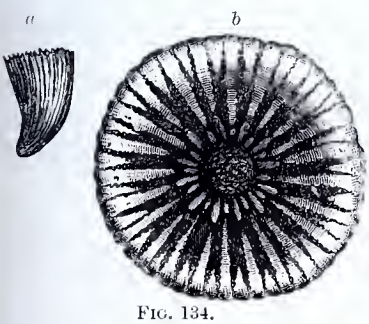


Fig. 134.

Trochocyathus conulus, From. Aptian; Haute Marne. *a*, Profile, natural size; *b*, Calice enlarged.

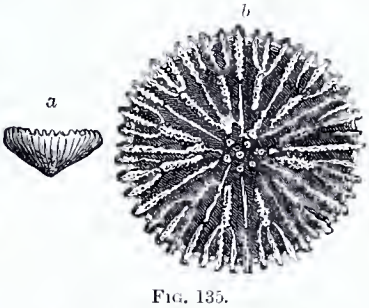


Fig. 135.

Deltocyathus Italicus, E. and H. Miocene; Porzteich, Moravia. *a*, Profile, natural size; *b*, Calice enlarged.

Fig. 136.

Caryophyllia cyathus, Sol. Recent. Longitudinal section, natural size (after Milne-Edwards).

Flabellum, Lesson. (Fig. 133). Wedge-shaped, compressed, isolated, or attached. Septa numerous. Wall covered with epitheca, and sometimes furnished with spinous processes. Tertiary and Recent.

Trochocyathus, E. and H. (Fig. 134). Horn-shaped, with circular calice. Septa stout; columella papillous and trabecular, and surrounded by several cycles of pali. Numerous species from Lias to Recent.

Thecocyathus, E. and H. Depressed, conical, or discoidal, attached early in life, later becoming free. Wall with thick epithecal investment. Calice circular, septa numerous; columella fasciculate, and surrounded by several cycles of pali. Lias, Jurassic, Cretaceous, and Recent.

Paracyathus, *Deltocyathus*, E. and H. Tertiary and Recent. *Discocyathus*, E. and H. Jurassic. *Coenocyathus*, *Acanthocyathus*, *Bathycyathus*, E. and H., etc. Tertiary and Recent.

Caryophyllia, Stokes (Fig. 136). Turbinate, with broad base, attached. Calice circular; columella papillous, trabecular, and surrounded by a single cycle of pali. Cretaceous to Recent.

Family 2. **Oculinidae.** Milne-Edwards and Haime.

Invariably composite coralla, increasing by lateral gemmation. Walls of corallites thickened by a compact coenenchyma. Lower portion of visceral chamber narrowed or filled up by deposition of stereoplasma. Septa moderately numerous; interseptal loculi usually open to the base. Lias to Recent; fossil forms not particularly numerous.

Oculina, Lam. Corallites irregularly or spirally distributed over the smooth surface of coenenchyma. Septa slightly projecting; columella papillous, surrounded by cycle of pali. Tertiary and Recent.

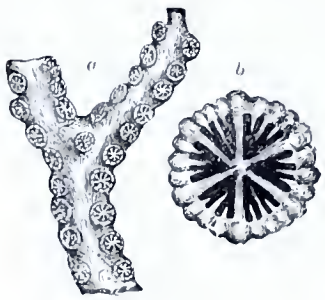


Fig. 137.

Enallohelia striata, Quenst. Coral-Rag; Nattheim. *a*, Natural size; *b*, Calice enlarged.

Agathelia, Reuss. Like the preceding, but forming tuberous or lobate colonies. Cretaceous and Tertiary.

Synhelia, E. and H. Cretaceous. *Astrohelia*, E. and H. Tertiary. *Psammohelia*, *Euhelia*, E. and H., etc. Jurassic.

Haplohelia, Reuss. Small, arborescent, with corallites all disposed on one side of the branches. Coenenchyma striated or granulated. Septa in three cycles; columella and pali present. Oligocene.

Enallohelia, E. and H. (Fig. 137). Stock branching; corallites disposed usually in alternating sequence in two rows along the sides of branches. Coenenchyma highly developed, striated, or granulated; columella rudimentary. Jurassic.

Family 3. **Pocilloporidae.** Verrill.

Composite, branching, lobate, or massive colonies, with small cylindrical corallites, united by compact coenenchyma. Septa few (6-24), *sometimes rudimentary. Visceral chamber partitioned off by horizontal tabulae.*

Of the two recent genera belonging to this family, *Pocillopora* and *Seriatopora*, Lam., the former occurs also fossil in the Tertiary.

Family 4. **Stylophoridae.** Milne-Edwards and Haime.

Composite coralla, with corallites united by vesicular or compact coenenchyma. Septa well developed, forming a central columella; interseptal loculi empty throughout. Jurassic to Recent.

Stylophora, Schweig. (Fig. 138). Stock branching, or depressed, massive, and tuberous. Calices small, embedded in abundant, at the surface spinous, coenenchyma. Septa well developed, moderately numerous; columella styliform. Jurassic, Tertiary, and Recent.

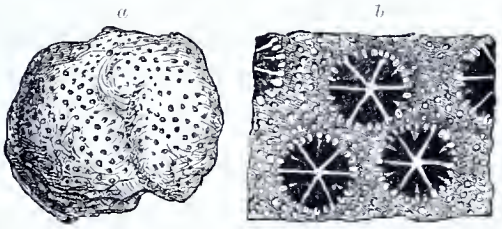


Fig. 138.

Stylophora subreticulata, Reuss. Miocene; Grund, near Vienna. *a*, Corallum, natural size; *b*, Surface greatly enlarged.

Araeacis, E. and H. Eocene. *Stylohelia*, E. and H. Jurassic and Cretaceous.

Family 5. **Astraeidae.** Milne-Edwards and Haime.

Corallum composite, or more rarely simple. Theca formed by fusion of septal edges. Septa numerous, usually well developed; visceral chamber partitioned off by more or less abundantly developed dissepiments, more rarely by tabulae. Multiplication by budding or fission. Corallites of massive colonies usually reaching considerable altitude, and united with one another either directly by the walls or by means of septa exothecally produced (costal septa).

Very abundant from the Trias onwards, and by far the most protean family of all the *Hexacoralla*. According to the serrated or entire character of the free septal edges, Milne-Edwards divides the *Astraeidae* into two sub-families—the *Astraeinae* and the *Eusmiliinae*.

Sub-Family A. Astraeinae. Milne-Edwards and Haime.

Upper septal edges toothed, serrated, or lobular.

a. Simple coralla.

Montlivaultia, Lamx. (Fig. 139).[1] Cylindrical, conical, turbinate, or discoidal, and either acutely pointed, or broadly expanded at the base. Septa

Fig. 139.

Montlivaultia caryophyllata, Lamx. sp. Great Oolite; Caen, Calvados. Natural size.

Fig. 140.

Leptophyllia sinuosa, From. Neocomian; St. Dizier, Haut-Marne. Natural size.

numerous, upper edges serrated. Columella absent; epitheca thick, corrugated, readily becoming detached. Common in Triassic and Jurassic; somewhat rare in Cretaceous and Tertiary.

Leptophyllia, Reuss (Fig. 140). Like the preceding, but without epitheca, and attached by broad base. Jurassic and Cretaceous.

Lithophyllia, E. and H. Like the preceding, but with vesicular columella. Miocene and Recent.

β. Simple coralla or composite colonies multiplying by calicinal or marginal gemmation.

Stylophyllum, Reuss. Corallum simple, either with or without calicinal or marginal gemmation, or forming massive colonies. Septa stout, but only inferiorly complete, terminating above in strong vertical spines. Dissepiments vesicular; wall covered with epitheca. Alpine Trias.

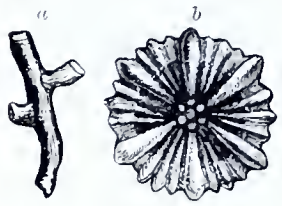


Fig. 141.

Stylocora exilis, Reuss. Miocene; Niederleis, Austria. *a*, Corallum in natural size. *b*, Calice enlarged (after Reuss).

Stylophyllopsis, Frech. Simple or imperfectly branching. Septa terminating near the centre in detached vertical spines. Alpine Trias.

γ. Bushy colonies multiplying by lateral gemmation.

Cladocora, Ehrbg. Corallum composed of long cylindrical branches, free on all sides. Calice circular; septa well developed; columella papillous; cycle of pali present. Jurassic to Recent.

Stylocora, Reuss (Fig. 141). Branches cylindrical; septa stout, those of the first cycle with columnar thickenings on inner edges; columella styliform. Cretaceous and Miocene.

Pleurocora, E. and H. Cretaceous. *Goniocora*, E. and H. Triassic and Jurassic.

δ. Composite corallites multiplying by basal gemmation; buds arising from stolons or basal expansions.

Rhizangia, E. and H. (Fig. 142). Corallites united by short, sub-cylindrical stolons. Calices shallow, circular; columella papillous. Cretaceous and Tertiary.

Latusastraea, d'Orb. Corallites arising from common basal expansion, short and strongly inclined to one side, so that the calices acquire a semicircular contour and assume the form of protruded lips. Jurassic and Cretaceous.

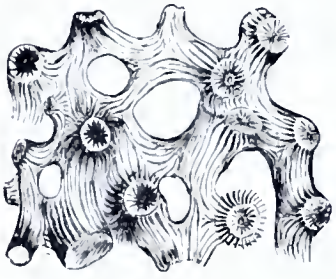


Fig. 142.

Rhizangia Michelini, Reuss. Middle Cretaceous; Gosau Valley, Austria. Natural size (after Reuss).

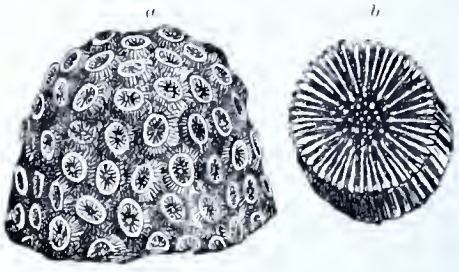


Fig. 143.

Cladangia conferta, Reuss. Miocene; Bischofswart, Moravia. *a*, Corallum, natural size; *b*, Calice enlarged (after Reuss).

Astrangia, *Cryptangia*, *Phyllangia*, *Cladangia*, *Ulangia*, E. and H, etc. Tertiary and Recent.

ε. Massive coralla multiplying by lateral gemmation.

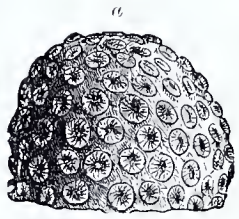
Heliastraea, E. and H. (Fig. 144). Cylindrical corallites united by exothecally produced, confluent, costal septa. Columella spongy; dissepiments numerous between the septa both within and exterior to the theca. Jurassic to Recent.

Plesiastraea, From. Like the preceding, but with several pali in front of all the cycles excepting the last. Tertiary and Recent.

Isastraea, E. and H. (Fig. 145). Corallites prismatic, closely crowded, and with fused walls. Calices polygonal; columella imperfect or absent. Trias to Cretaceous.

Latimaeandra, d'Orb. (Fig. 146). Like the preceding, but with the calices situated in short furrows. Trias to Cretaceous.

Stylastraea, From. Lias. *Amphiastraea*, From. Upper Jurassic. *Leptastraea*, *Solenastraea*, *Prionastraea*, E. and H., etc. Tertiary and Recent.



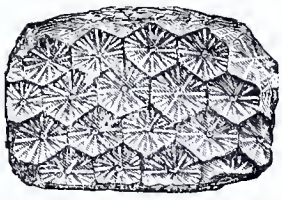


Fig. 145.

Isastraea helianthoides, Goldf. sp. Coral-Rag; Nattheim. Natural size.

Fig. 144.

Heliastraea conoidea, Reuss. Miocene; Enzesfeld, near Vienna. *a*, Corallum, natural size; *b*, Calices enlarged.

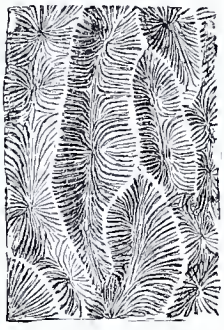


Fig. 146.

Latimaeandra seriata, Beck. Coral-Rag; Nattheim. Natural size (after Becker).

ζ. *Massive coralla multiplying by fission.*

Favia, Oken (Fig. 147). Corallum massive; calices oval or distorted, and united by confluent costal septa; columella spongy. Jurassic to Recent.

Goniastraea, E. and H. Corallites prismatic, calices polygonal. Septa well developed; columella spongy; pali in front of all cycles excepting the last. Cretaceous to Recent.

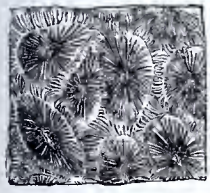


Fig. 147.

Favia caryophylloides, From. Coral-Rag; Nattheim. Natural size.

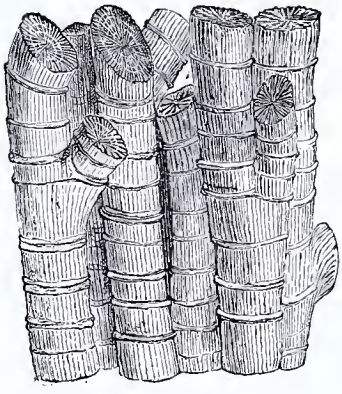


Fig. 148.

Calamophyllia Stokesi, E. and H. Coral-Rag; Steeple Ashton, England. Natural size.

Fig. 149.

Thecosmilia trichotoma, Goldf. sp. Coral-Rag; Nattheim. Natural size.

η. *Branching coralla multiplying by fission.*

Calamophyllia, Blainv. (*Rhabdophyllia*, E. and H.; *Lithodendron*, p. p. Mich.), (Fig. 148). Colony fasciculate or bushy; corallites very long, cylindrical.

Wall costate, without epitheca; columella absent. Trias, Jurassic, and Tertiary. Especially common in Alpine Trias. *C. clathrata*, Emmrich sp.

Thecosmilia, E. and H. (Fig. 149). Colony bushy, calices dividing by fission, and more or less free. Epitheca corrugated, readily wearing away; columella absent or rudimentary. Trias to Tertiary. According to Frech identical with *Calamophyllia*. Very common in Triassic and Jurassic.

Baryphyllia, From. *Hymenophyllia*, E. and H., etc. Cretaceous.

θ. Coralla with confluent calices increasing by fission.

Leptoria, E. and H. (Fig. 150). Corallum massive, composed of labyrinthic rows of confluent corallites with fused walls. Septa closely crowded, approaching parallelism; columella foliaceous. Jurassic to Tertiary.

Fig. 150.

Leptoria Konincki, Reuss. Upper Cretaceous; Gosau Valley. Natural size.

Fig. 151.

Aspidiscus cristatus, König. Middle Cretaceous; Batna, Algeria. Natural size.

Diploria, E. and H. Like the preceding, but with corallites united by produced costal septa instead of directly by their walls. Cretaceous to Recent.

Aspidiscus, König. (Fig. 151). Corallum discoidal, circular, or elliptical, covered on lower side with wrinkled epitheca. Calicinal furrows radiating from the centre outwards, and separated from one another by sharply crested ridges. In the centrifugally disposed corallites the outermost septa are thickened, and form by their union a banded margin. Cretaceous.

Stiboria, Etall. Jurassic. *Stelloria*, d'Orb. Cretaceous. *Macandrina*, Lam. Cretaceous to Recent. *Symphyllia*, E. and H. Tertiary and Recent.

Sub-Family B. Eusmilinae. Milne-Edwards and Haime.

Upper septal edges entire, not serrated.

a. Simple coralla.

Trochosmilia, E. and H. (Fig. 152). Turbinate, base acutely pointed or

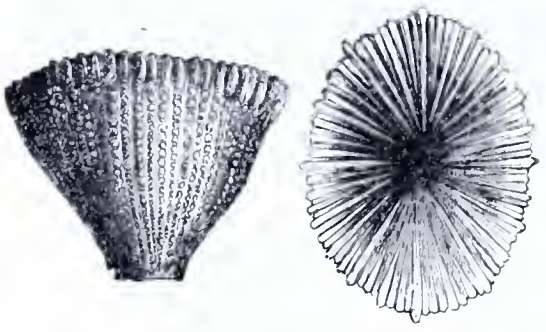


Fig. 152.

Trochosmilia granifera, Raime. Turonian; Bains-de-Rennes, France. *a*, Profile; *b*, Calice slightly enlarged (after Fromentel).

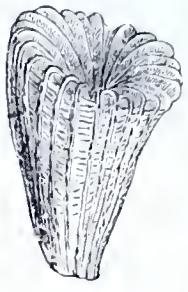


Fig. 153.

Coelosmilia laxa, E. and H. White Chalk; Lüneburg, Hanover. Natural size.

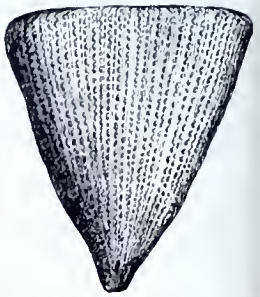


Fig. 154.

Placosmilia cuneiformis, E. and H. Upper Cretaceous; St. Gilgen on Wolfgangsee, Austria. Natural size.

encrusting. Septa numerous, extending to the centre. Wall without epitheca,

costae granulated. Columella absent, dissepiments numerous. Cretaceous and Tertiary.

Coelosmilia, E. and H. (Fig. 153). Like the preceding, but with dissepiments sparsely developed. Cretaceous and Recent.

Placosmilia, E. and H. (Fig. 154). Cuneiform, base acutely pointed or slightly pedunculate. Calice laterally compressed, elongated. Septa numerous; dissepiments abundant; columella foliaceous. Epitheca absent; costae granulated. Cretaceous.

Diploctenium, Goldf. Calice laterally compressed, greatly elongated in transverse direction, and bent downwards at the ends so as to become crescent-shaped. Columella and epitheca absent. Costae dichotomously or trichotomously furcate. Upper Cretaceous.

Axosmilia, E. and H. Jurassic. *Phyllosmilia*, From. Cretaceous. *Lophosmilia*, E. and H. Cretaceous and Recent.

β. Corallu multiplying by lateral gemmation.

Placophyllia, d'Orb. (Fig. 155). Buds originating on calicinal margin or sides, and giving rise to bushy or massive colonies. Columella styliform. Jurassic.

Galaxea, Oken. Bushy colonies with cylindrical corallites united by layers of finely vesicular epitheca (*peritheca*). Recent.

Stylina, Lam. (Fig. 156). Massive colonies, with corallites united by coalescent costae. Septa well developed, disposed in six, eight, or ten cycles.

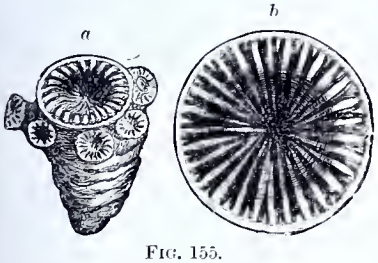


FIG. 155.

Placophyllia dianthus, Goldf. sp. Coral-Rag; Nattheim. *a*, Corallum, natural size; *b*, Calice enlarged.

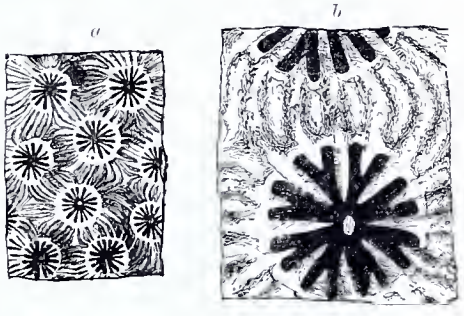


FIG. 156.

Stylina Delabechei, E. and H. Coral-Rag; Steeple Ashton, England. *a*, Natural size; *b*, Calices enlarged.

Dissepiments numerous; columella styliform. Multiplication by costal gemmation. Profuse in Trias, Jurassic, and Cretaceous.

Placocoenia, d'Orb; *Cryptocoenia*, E. and H. Jurassic and Cretaceous.

Cyathophora, Mich. Massive colonies, with corallites united by costae. Septa short, not reaching the centre; columella absent. Visceral chamber partitioned off by horizontal tabulae. Jurassic and Cretaceous.

Coccophyllum, Reuss. Massive colonies, with corallites united directly by their walls. Calices polygonal, septa numerous. Columella absent; visceral chamber tabulated. Alpine Trias.

Pinacophyllum, Frech. Triassic.

Holocystis, Lonsd. Massive colonies, with corallites united by costae. Four of the septa larger or stouter than the rest. Tabulae in visceral chamber. Cretaceous.

Astrocoenia, E. and H. (Fig. 157). Massive colonies. Corallites polygonal, united by their walls; septa numerous, long. Columella styliform; only dissepiments present in visceral chamber. Trias to Tertiary.

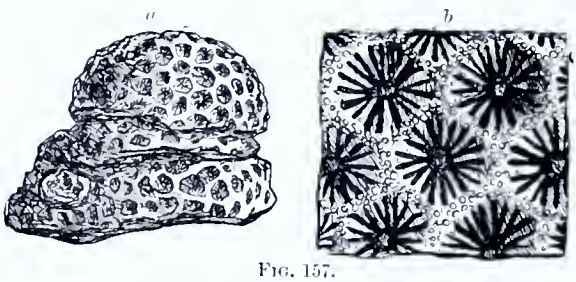


Fig. 157.

Astrocoenia decaphylla, E. and H. Upper Cretaceous; Gosau Valley, Austria. *a*, Corallum, natural size; *b*, Calices enlarged.

Stephanocoenia, E. and H. Like the preceding, but with columella surrounded by cycle of pali. Trias to Recent.

Phyllocoenia, E. and H. (*Confusastraea*, d'Orb.; *Adelastraea*, Reuss). Massive colonies. Corallites round or oval, imperfectly united by costae. Septa strongly developed, thickened in the middle between theca and the centre. Columella rudimentary. Trias to Tertiary.

Convexastraea, d'Orb.; Trias to Cretaceous. *Columnastraea*, *Stylocoenia*, E. and H., etc.; Cretaceous and Tertiary.

γ. Coralla multiplying by fission.

Haplosmilia, d'Orb. Bushy colonies. Corallites usually with dichotomously dividing crests. Calices circular or elongated; columella styliform; theca with ridge-like costae. Jurassic.

Plocophyllia, Reuss (Fig. 158). Branching, foliaceous, or massive colonies.

Fig. 158.

Plocophyllia calycularis, Reuss. Oligocene; Monte Carlotta, near Vicenza. Natural size.

Fig. 159.

Rhipidogyra crassa, From. Coral-Rag; Gray, Haute-Saône. 1/2 natural size.

Corallites either becoming free or grouped into detached rows. Columella absent. Tertiary.

Barysmilia, E. and H. Corallum massive, forming a thick stem, the apex of which is covered with short buds. Calices oval, sometimes disposed in series; columella rudimentary. Cretaceous.

Stenosmilia, From. Like the preceding, but with lamellar columella. Cretaceous.

Pachygyra, E. and H. Corallites arranged in winding rows, and united by

broad mass of costal coenenchyma. Columella lamellar. Jurassic and Cretaceous.

Phytogyra, d'Orb. Jurassic and Cretaceous.

Rhipidogyra, E. and H. (Fig. 159). Corallum fan-shaped, often corrugated, and with but a single calicular furrow. Columella lamellar. Jurassic and Cretaceous.

Family 6. **Fungidae**. Milne-Edwards and Haime.

Simple coralla, or low, laterally expanding colonies. Septa numerous, upper edges serrated; synapticula (rarely also dissepiments) between the septa. Wall between individual corallites absent, but developed on under side of colonies. Reproduction sexual or by gemmation. Jurassic to Recent.

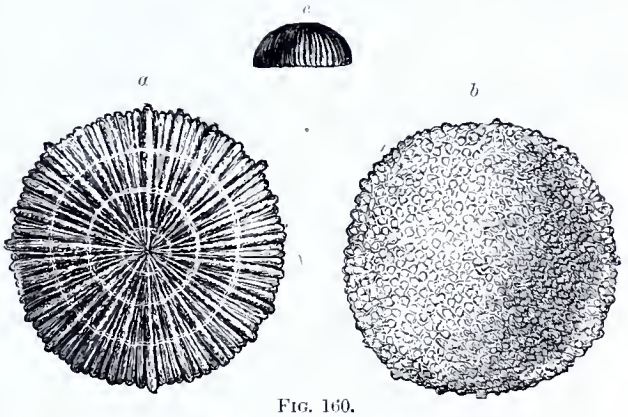


Fig. 160.

Microseris hemisphaerica, From. Greensand (Cenomanian); Le Mans, France. *a* and *b*, Upper and lower surfaces, enlarged; *c*, Profile, natural size.

Fungia, Lam. p.p. emend. Dana. Corallum simple, depressed, discoidal. Septa very numerous, varying in length and thickness, united only by synapticula, and projecting on the lower side as dentated costae. Theca absent. Post-pliocene and Recent.

Microseris, From. (Fig. 160). Corallum simple, discoidal, circular; upper side vaulted, lower flat and granulated. Cretaceous.

Trochoseris, E. and H. Tertiary and Recent.

Cyathoseris, E. and H. (Fig. 161). Corallum turbinate, attached. Young

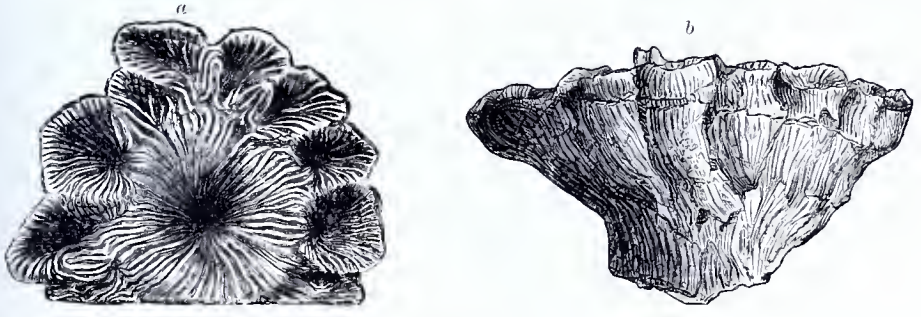


Fig. 161.

Cyathoseris subregularis, Reuss. Oligocene; Monte Carlotta, near Vicenza, Italy. *a*, Top view; *b*, Side view, natural size.

corallites arising from periphery by costal gemmation. Common outer wall naked, striated. Cretaceous and Tertiary.

Lophoseris, E. and H.; *Mycedium*, Oken; *Agaricia*, Lam., etc. Tertiary and Recent.

Sub-Order B. PERFORATA. Milne-Edwards and Haime.

Skeleton built up of small calcareous bodies (sclerites), between which are empty interstices of greater or lesser size. Theca formed by fusion of outer septal edges or absent. Interseptal loculi empty throughout or traversed by synapticula or dissepiments.

? Family 1. Archaeocyathidae.[1] Walcott.

Simple, turbinate, or sub-cylindrical coralla. Septa and theca porous; inner septal edges united by perforated interior wall, which encloses a hollow central space. Synapticula present in interseptal loculi.

All the genera described up to the present time (*Archaeocyathus*, Bill.; *Ethmophyllum*, Meek; *Spirocyathus*, Hinde; *Protopharetra*, Bornem., etc.) are restricted to the Cambrian rocks of Canada, North America, Spain, and Sardinia. They represent possibly a distinct order of the *Madreporaria*.

Family 2. Eupsammidae. Milne-Edwards and Haime.

Corallum simple or becoming composite by lateral gemmation. Septa very numerous, sometimes united by synapticula, and frequently with their inner edges fused together. Theca naked or covered with epitheca, and formed by thickening of the septal edges. Silurian to Recent.

Calostylis, Linds. Corallum simple, sub-cylindrical, or composite and multiplying by lateral gemmation. Septa very numerous, of spongy consistency, and either fused together or united by synapticula. Columella thick, spongy; wall covered with epitheca. Silurian; Gottland.

Fig. 162.

Eupsammia trochiformis, Pallas. Calcaire Grossier; Chaussy, near Paris. Natural size.

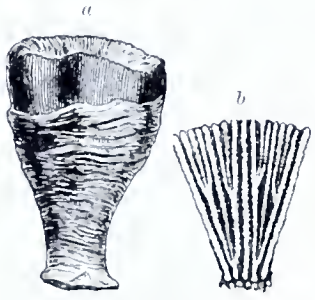


Fig. 163.

Balanophyllia sinuata, Reuss. Oligocene; Waldbockelheim, Prussia. *a*, Natural size; *b*, Number of septa enlarged.

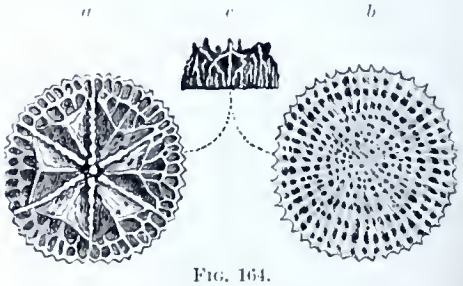


Fig. 164.

Stephanophyllia elegans, Bronn sp. Pliocene; Stazzano, near Modena, Italy. *a* and *b*, Upper and lower surfaces, enlarged; *c*, Profile, natural size.

Haplaraea, Milasch. Simple, cylindrical coralla, with broad encrusting base. Septa numerous, extending to the centre, perforated by large apertures, and sometimes fused together or united by synapticula. Traversa also present, but no columella. Jurassic and Cretaceous.

[1] *Billings, E.*, Palaeozoic Fossils of Canada, I., 1861-65.—*Walcott, C. D.*, Bull. U. S. Geol. Survey, No. 30, 1886.—*Bornemann, J. G.*, Versteinerungen des Cambrischen Systems von Sardinien, 1886.—*Hinde, G. J.*, Quart. Journ. Geol. Soc. vol. XLV., 1889. p. 125.

Eupsammia, E. and H. (Fig. 162). Conical or turbinate, acutely pointed, free. Septa very numerous, arranged in five cycles, those of the last cycle stouter than the rest. Columella present or absent. Eocene to Recent.

Balanophyllia, Wood (Fig. 163). Simple, subcylindrical, with broad encrusting base. Columella spongy; septa closely crowded, partly fused together. Eocene to Recent.

Stephanophyllia, Mich. (Fig. 164). Simple, discoidal; base horizontal, calice circular. Septa numerous; the six principal septa extending to the centre, the remainder with fused inner edges. Cretaceous and Tertiary.

Dendrophyllia, Blv. (Fig. 165). Corallum branching, increasing by lateral gemmation. Calices oval; septa numerous and slender, those of the last cycle extending to the spongy columella, and fused with the converging ends of shorter septa of preceding cycle. Tertiary and Recent.

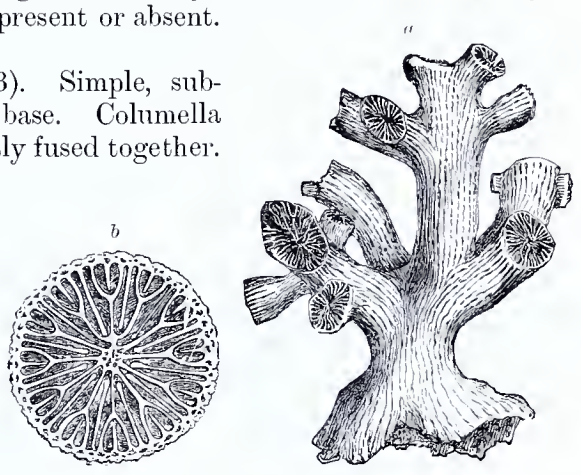


Fig. 165.

Dendrophyllia elegans, Duncan. Oligocene; Brockenhurst, England. *a*, Corallum, natural size; *b*, Transverse section of calice, enlarged.

Lobopsammia, *Stereopsammia*, E. and H.; Eocene. *Astroides*, E. and H.; Recent.

Family 3. **Thamnastraeidae**. Reuss.

(*Pseudoastraeidae* and *Pseudoagaricinae*, Pratz.)

Simple coralla, or composite, basally expanded or massive colonies. Septa numerous, more or less perforate, and composed of calcareous bodies (trabeculae) arranged in vertical or fan-shaped rows. Theca between individual corallites absent, but present on under side of corallites or on lower side of the common stock. Interseptal loculi with synapticulae and dissepiments. Abundant from Trias to Cretaceous; rarer in Tertiary and Recent.

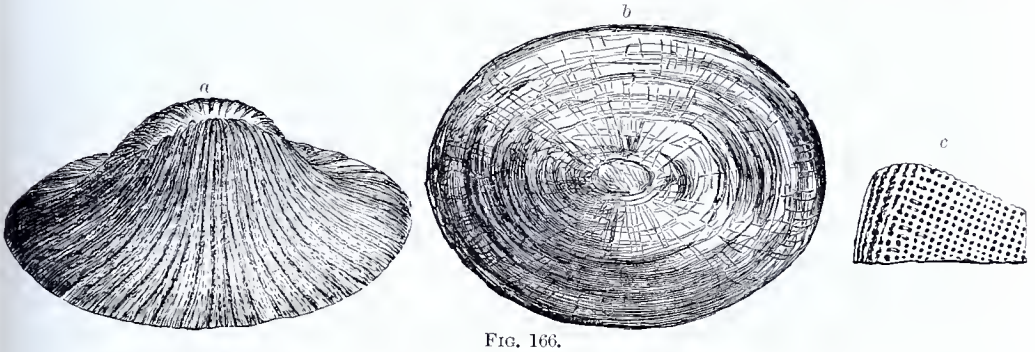


Fig. 166.

Cyclolites undulata, Lam. Upper Cretaceous; Gosau Valley, Salzkammergut. *a*, Side view; *b*, Lower surface; *c*, Lateral aspect of septum, natural size.

Anabacia, E. and H. Simple, free, discoidal, or lenticular coralla, with flat base. Upper side vaulted, calice slit-like. Septa very numerous, thin, and united by synapticulae. Theca absent. Jurassic.

Genabacia, E. and H. Like the preceding but composite, the central calice being surrounded by a row of smaller calices. Jurassic.

Microbacia, E. and H. Cretaceous.

Omphalophyllia, Laube. Simple, turbinate, or sub-cylindrical, attached, and covered with epitheca. Septa very numerous, upper edges granulated. Calice shallow, columella styliform. Alpine Trias.

Cyclolites, Lam. (Fig. 166). Simple, free, discoidal, upper side vaulted, lower flat and covered with corrugated epitheca. Septa very thin, extending

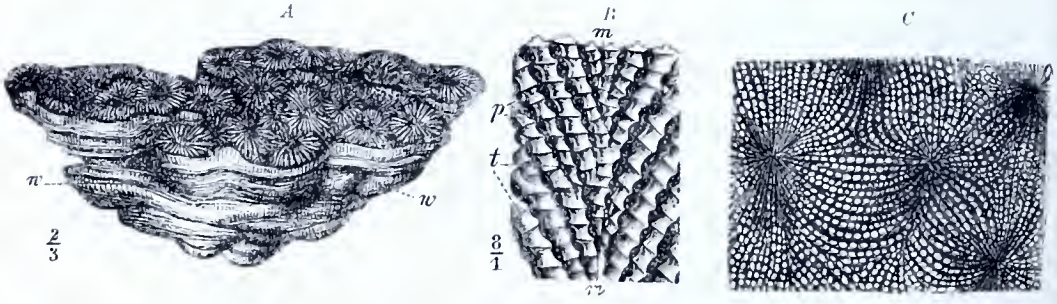


Fig. 167.

Thamnastraea prolifera, Becker. Upper Jurassic; Natthein, Württemberg. *A*, Corallum, 2/3 natural size; *w*, Common wall. *B*, Lateral surface of costal septum, enlarged (8/1), showing trabecular constitution; *m*, Line of junction of two septa belonging to different coralites; *t*, Trabeculae; *p*, Trabecular lacunae (after Pratz). *C*, *Thamnastraea agaricites*, Goldf. Upper Cretaceous; Gosau, Salzkammergut. Portion of upper surface of corallum, natural size.

to the centre, extremely numerous, composed of vertical rows of trabeculae, and united by synapticulae and dissepiments. Very abundant in Cretaceous, rare in Jurassic and Eocene.

Thamnastraea, Le Sauvage (Fig. 167). Composite, laterally expanded and pedunculate, or mushroom-shaped coralla. Common wall restricted to lower side of corallum; individual corallites without proper walls, but united by costal septa. Columella styliform or rudimentary. Septa well developed, composed of fan-shaped rows of cylindrical trabeculae, and united by synapticulae and dissepiments. Very abundant from Trias to Oligocene.

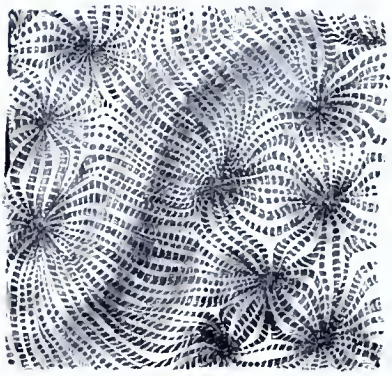


Fig. 168.

Comoseris confertа, Reuss. Oligocene; Monte Carlotta, near Vicenza. Twice enlarged.

Dimorphastraea, d'Orb. Like the preceding, but with calices concentrically arranged about a central individual. Trias to Tertiary.

Comoseris, d'Orb. (Fig. 168). Like *Thamnastraea*, but with calices separated into groups by ascending flexuous ridges. Jurassic and Tertiary.

Astraeomorpha, Reuss. Coralla composite, tuberous, basally expanded, or branching, and covered with corrugated epitheca. Corallites small, united by short and stout costal septa; columella styliform. Trias to Oligocene.

Microsolena, Lamx.; Trias and Jurassic. *Dimorpharaea*, From.; Jurassic.

Family 4. **Poritidae.** Dana.

Composite coralla composed of porous sclerenchyma. Corallites small; septa as a rule only moderately numerous, sometimes represented by rows of trabeculae or lamellae. Theca absent.

Sub-Family A. Spongiomorphinae. Frech.

Corallum composed of thick trabeculae and strengthened by horizontal synapticulae. Calices very imperfectly differentiated from coenenchyma, and without distinct septa. Dissepiments usually sparsely developed.

Of the genera belonging to this sub-family, *Spongiomorpha*, *Heptastylis*, and *Stromatomorpha*, Frech, are found in the Alpine Trias (Rhaetic and Zlambach Schichten). These are all tuberous, composite coralla of extremely irregular form. In *Spongiomorpha* and *Heptastylis*, six septa are indicated by somewhat regularly disposed columns of trabeculae; and in the latter form these are bound together by synapticulae which are projected at equal altitudes, and form perforated horizontal storeys. In *Stromatomorpha* no radial arrangement of the trabecular septa exists.

Palaeacis, E. and H. (*Sphenopoterium*, Meek and Worth), occurring in the Carboniferous limestone of North America and Scotland, possibly also belongs here.

Sub-Family B. Turbinarinae. Milne-Edwards and Haime.

Septa well developed, compact. Corallites embedded in canaliculated coenenchyma.

Actinacis, d'Orb. (Fig. 169). Massive or branching coralla. Coenenchyma abundant, granulated; septa stout, of nearly uniform proportions, columella papillous; pali in front of all the septa. Cretaceous and Tertiary.

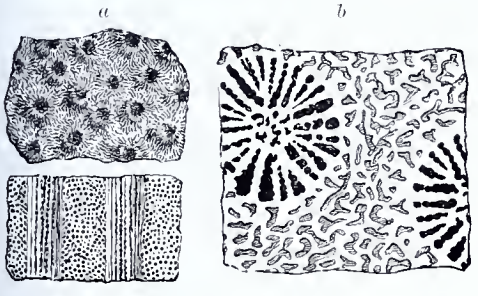


Fig. 169.

Actinacis elegans, Reuss. Upper Cretaceous; Oosau Valley, Salzkammergut. *a*, Upper surface, natural size; *b*, Transverse section, enlarged; *c*, Longitudinal section, enlarged (after Reuss).

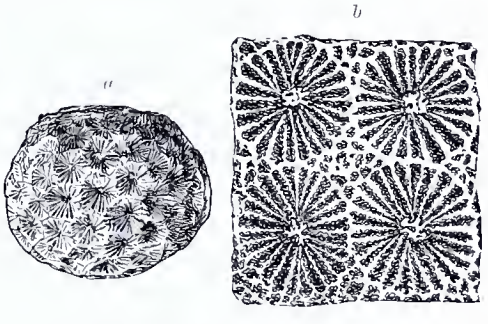


Fig. 170.

Litharaea Websteri, Bowerb. sp. Eocene; Bracklesham Bay, England. *a*, Corallum, natural size; *b*, Four calices enlarged.

Astraeopora, Blv. Massive coralla. Coenenchyma porous and on upper surface echinulate. Septa of dissimilar proportions; columella and pali absent. Tertiary and Recent.

Dendracis, E. and H.; *Cryptaxis*, Reuss. Tertiary.

Turbinaria, Oken (*Gemmipora*, Blv.) Corallum foliaceous. Coenenchyma tolerably compact and finely echinulate. Septa of similar proportions; columella spongy. Cretaceous to Recent.

Sub-Family C. Poritinae. Milne-Edwards and Haime.

Septa not very numerous, well developed. Corallites united by their porous walls.

Litharaea, E. and H. (Fig. 170). Massive coralla. Calices sub-polygonal; septa generally in three cycles; columella spongy. Eocene and Miocene.

Rhodaraea, E. and H. Massive coralla. Spurious walls of corallites thick; pali prominent. Miocene and Recent.

Porites, Lam. (Fig. 171). Massive or branching coralla. Calices shallow, polygonal; septa irregularly reticulated; columella papillous, surrounded by single cycle of pali. Cretaceous to Recent. The genus *Porites* is one of the most important of existing reef-builders.

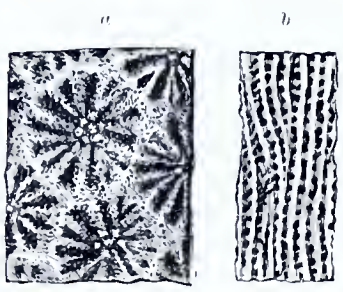


Fig. 171.

Porites incrustans, Reuss. Miocene; Moravia. *a*, Transverse section; *b*, Longitudinal section. Both figures highly magnified.

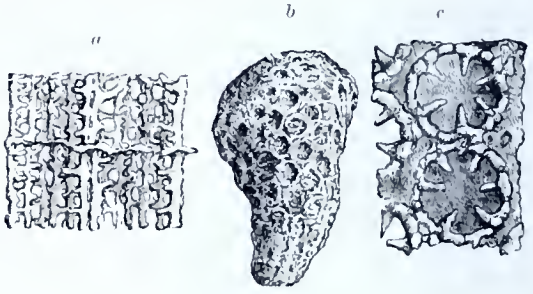


Fig. 172.

a, *Alveopora spongiosa*, Dana. Recent; Fiji Islands. Longitudinal section of corallite showing perforate walls and tabulae; *b*, *Alveopora rudis*, Reuss. Nummulitic limestone; Oberburg, Styria, $^1/_1$; *c*, Calices, greatly enlarged. (Fig. *a*, after Dana; *b*, after Reuss).

Protaraea and *Stylaraea*, E. and H. Usually encrusting coralla with polygonal calices. Visceral chambers partitioned off by horizontal tabulae. Silurian and Devonian.

Sub-Family D. Alveoporinae. Verrill.

Septa composed of detached trabeculae, spines, or reticulated lamellae. Theca perforate. Visceral chamber with perforate tabulae.

Alveopora, Quoy and Gaim. (Fig. 172). Massive coralla. Calices small, polygonal. Septa represented by detached spinous processes. Tabulae sparsely developed, remotely situated. Tertiary and Recent.

Koninckia, E. and H. Cretaceous.

Family 5. **Madreporidae.** Dana.

Composite, branching, or lobate coralla with small tubiform corallites embedded in a canaliculated and reticulated coenenchyma. Septa (6-12) *sometimes imperfectly developed. Two long septa projected from opposite sides and meeting in the centre.*

The genus *Madrepora*, Lin. (Fig. 173), is an important agent in the construction of existing coral reefs, and builds colonies sometimes of considerable size. It occurs sparsely in the fossil state in the Tertiary.

Range and Distribution of the Hexacoralla.

The group *Aporosa* of the *Hexacoralla* appears to have originated from the *Tetracoralla*, and to form the direct continuation of their line. They begin as

the latter disappear; they develop a great variety of forms in the Trias, and from the Mesozoic down to the present day they have continued to play a leading part in the construction of coral-reefs. Of the six families constituting the *Aporosa*, the *Astraeidae* is by all odds the most important and most protean, in comparison to which the *Fungidae*, *Stylophoridae*, *Pocilloporidae*, *Oculinidae*, and *Turbinolidae* fall into greatly subordinate rank. The other families are all younger than the *Astraeidae*, not beginning until the Jurassic, the *Pocilloporidae*, indeed, not until the Tertiary.

The *Perforata* constitute a well-defined branch of the *Hexacoralla*, whose ancestry may perhaps be sought in the remarkable *Archaeocyathidae* of the Cambrian. The *Eupsammidae* and *Poritidae* occur sporadically in the Silurian and Carboniferous, while it is not until the Trias that the *Thamnastraeidae* and *Poritidae* develop a large variety of forms; from the Trias to the Tertiary, however, these genera continue to be important reef-builders. The *Eupsammidae* attain their greatest development in the Tertiary and Recent, while the *Madreporidae* belong almost exclusively to the present period.

Occasional isolated deep-sea forms are met with in most of the several geological periods, but the usual mode of occurrence of the *Hexacoralla* is associated in masses in coralline limestones; the limestones may be of very variable thicknesses, but as a rule are interstratified between deposits of distinctly littoral character. Ancient coral-reefs most nearly resemble modern fringing or barrier reefs, but not atolls, the origin of which is clearly dependent upon the peculiar orographic conditions of the Pacific Ocean.

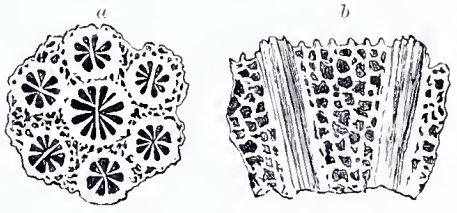


FIG. 173.

Madrepora Anglica, Duncan. Oligocene; Brockenhurst, England. *a*, Calices enlarged; *b*, Longitudinal section, greatly enlarged.

The St. Cassian, Zlambach, and Rhaetic beds of the Alpine Trias contain large numbers of reef-building *Hexacoralla;* but the pure limestones and dolomites of the Alps, as well as the Trias outside the Alpine region, are frequently either almost or entirely destitute of coralline remains.

In the Lias coral-reefs have been found in England, Luxemburg, and Lorraine. Certain beds of the Dogger, usually of but meagre thickness, are occasionally charged with corals, as in Swabia, the Rhine valley in Baden, the Swiss Jura, Normandy, and England. Coralline limestones are abundantly developed in the Upper Jurassic of the Jura Mountains in France and Switzerland, in Lorraine, Southern Baden, Swabia (Nattheim, Blaubeuern), Bavaria (Kelheim), many places in France and England, as well as in the whole province of the Alps, Carpathians, Cévennes, and Apennines; here the uppermost horizon (Tithonian) is especially characterised by their development.

In the Lower Cretaceous (Neocomian) coral-reefs are found in France (Haute-Marne and Yonne), Crimea, and Mexico; while the Urgonian of Switzerland and the Bavarian Alps is occasionally charged with corals. In the Turonian and Senonian of the Alps (Gosau Beds), Pyrenees, and the Provence, numerous coral-reefs occur, usually accompanied by *Rudistae;* elsewhere, however, except in Holland (Maestricht) and Denmark (Faxoe), the Upper Cretaceous contains but a limited number of reef-building *Hexacoralla.*

In the older Tertiary (Eocene and Oligocene) the occurrence of coral-reefs is restricted to the northern and southern flanks of the Alps and Pyrenees,

Arabia and the West Indies; while outside the Alps in Europe and in America their distribution is mostly sporadic. In the Miocene and Pliocene the true coral-reefs retreat more and more towards the equator (Red Sea, Java, Japan), while the *Hexacoralla* which persist in formations of the temperate zone (Vienna Basin, Italy, Touraine) constitute but an insignificant feature of the general fauna.

Appendix to the Hexacoralla.

Sub-Order C. TABULATA.[1] Milne-Edwards and Haime.

Invariably composite coralla composed of tubiform or prismatic corallites. Walls thick, independently calcified, compact, or perforated by connecting mural pores. Septa but slightly developed (usually six or twelve), sometimes represented merely by vertical ridges or rows of spines, and sometimes entirely absent. Visceral chamber partitioned off into successive storeys by tabulae. Synapticulae and dissepiments wanting.

To the *Tabulata* were originally assigned by Milne-Edwards and Haime all corals having numerous tabulae and rudimentary septa. Later researches have shown, however, that some of these forms (e.g. *Pocilloporidae*) belong to the *Aporosa*, others (*Helioporidae*) to the *Octocoralla*, and still others (*Millepora*) to the *Hydrozoa*; while the affinities of a few (*Chaetitidae, Monticuliporidae*) are of such doubtful nature as to be referred by some authors to the Corals, and by others to the Bryozoans. The majority of the typical *Tabulata* (*Favositidae, Syringoporidae, Halysitidae*) exhibit close relationships to the *Hexacoralla*; but since they are for the most part now extinct and are largely confined to the Palaeozoic rocks, the positive determination of their systematic position seems almost hopeless. The ontogeny of the corallites in the *Tabulata* shows that the development of mural pores is homologous with the process of gemmation. Reproduction sometimes takes place by fission, but generally by means of buds from the edges of the calices at various stages during the growth of the parent corallites. Buds are given off early in *Aulopora*, producing basal corallites only; periodically in *Romingeria*, producing verticils of corallites; periodically and on one side in *Halysites*, producing linear series of adjacent corallites; and very frequently in *Favosites*, etc., producing compact coralla with numerous mural pores representing aborted buds.

Family 1. Favositidae. Milne-Edwards and Haime.

Massive or branching coralla. Corallites uniformly prismatic, tall, and united by their walls, which are perforated by large-sized pores. Septa very short, usually represented by but faintly projecting ridges or rows of spines, but seldom completely absent. Tabulae numerous, situated at regular intervals, complete and horizontal, more rarely oblique or irregularly vesicular ("cystoid").

The *Favositidae* are distinguished from the *Poritidae*, with which Verrill associates them, by their thick, solid walls, which are punctured by round,

[1] *Lindström, G.*, Affinities of the Anthozoa Tabulata (Ann. Mag. Nat. Hist. Ser. 4, XVIII.), 1876. —*Dybowski, W.*, Die Chaetitiden der ostbaltischen Silurformation (Verh. der k. russ. min. Gesellsch. St. Petersburg), 1877.—*Nicholson, H. A.*, On the Structure and Affinities of the Tabulate Corals of the Palaeozoic Period. London, 1879.—On the Structure and Affinities of the genus Monticulipora. London, 1881.—*Roemer, F.*, Lethaea Palaeozoica, I., 1883, p. 416.—*Waagen, W.*, and *Wentzel, W.*, The Salt Range Fossils. Palaeontol. Indica, 1887.—*Haug, E.*, Ueber sogenannte Chaetetes aus mesozoischen Ablagerungen (Neues Jahrb. für Mineral.), 1883, I., p. 171.—*Beecher, C. E.*, The Development of a Palaeozoic Poriferous Coral.—Symmetrical Cell Development in the Favositidae. (Trans. Conn. Acad. vol. VIII.), 1891.

sometimes tubiform mural pores. The corallites are usually polygonal in contour, and their walls exhibit in transverse sections a dark, or sometimes light-coloured median line, with thickenings of stereoplasma on either side (Fig.

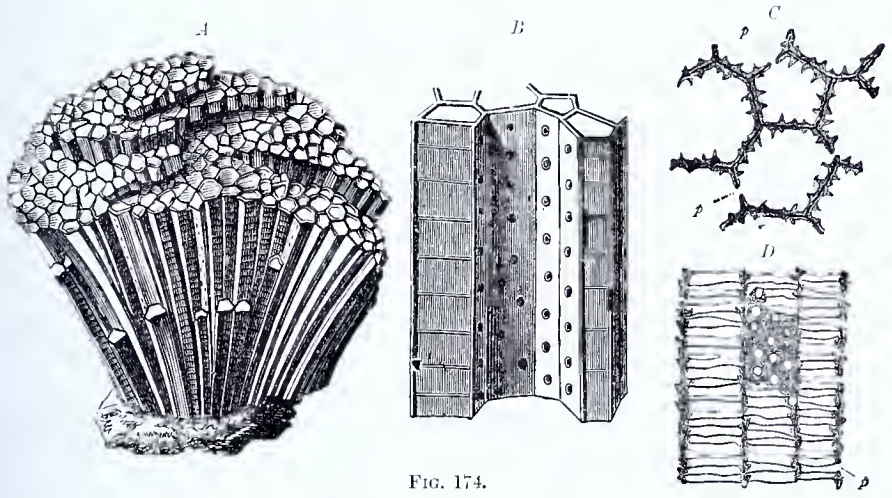


Fig. 174.

Favosites polymorpha, Goldf. sp. Devonian; Eifel. *A*, Corallum, natural size. *B*, Corallites enlarged, two of them broken open and showing tabulae. *C* and *D*, Transverse and longitudinal sections showing spiniform septa and mural pores (*p*). (*C* and *D* after Nicholson.)

174, *C*). The family is exclusively Palaeozoic, and plays an important part in the formation of Silurian, Devonian, and Carboniferous coralline limestones.

Favosites, Lam. (*Calamopora*, Goldf.), (Fig. 174). Corallum massive, more rarely branching. Corallites prismatic, polygonal, generally hexagonal. Mural pores distributed at considerable intervals. Septa very faintly developed, represented by longitudinal ridges or rows of spines, or occasionally obsolete. Tabulae numerous. Ordovician to Carboniferous; very abundant in Silurian and Devonian.

Columnopora, Nich. (*Calapoecia*, Bill.) Like the preceding, but with numerous, short, well-marked septa. Mural pores large, disposed in vertical rows between the septa. Ordovician.

Emmonsia, E. and H.; Ordovician to Carboniferous. *Nyctopora*, Nich.; Ordovician (Trenton). *Syringolites*, Hinde; Silurian (Niagara).

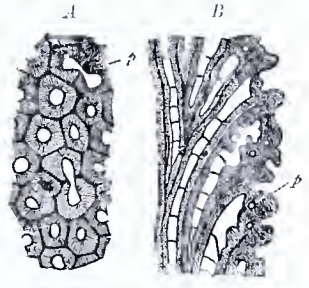


Fig. 175.

Pachypora Nicholsoni, Frech. Middle Devonian; Eifel. *A*, Transverse section. *B*, Longitudinal section, enlarged; *p*, Mural pores (after Nicholson).

Pachypora, Lind. (Fig. 175). Corallum branching, composed of prismatic, polygonal corallites, the walls of which are so thickened towards their mouths by layers of stereoplasma that the calices appear to have circular contours. Septa very minute; mural pores scanty, but often of large size. Abundant in Silurian and Devonian.

Fig. 176.

Striatopora flexuosa, Hall. Silurian (Niagara); New York.

Trachypora, E. and H. Dendroid with cylindrical stems. Corallites polygonal; walls so thickened by layers of stereoplasma that the calices become round and greatly contracted, and appear to be superficially widely separated. Mural pores few and irregularly distributed. Septa represented by rows of spines. Tabulae remote. Common in Devonian.

Striatopora, Hall (Fig. 176). Like the preceding, but with tubes contracted by stereoplasma at a greater depth, so as to give the calices a funnel-shaped appearance. Silurian and Devonian.

Alveolites, Lam. (Fig. 177). Corallum massive or branching, composed of small, contiguous, compressed, thin-walled corallites, with obliquely opening triangular or semilunar calices. Septa very faint, represented merely by ridges

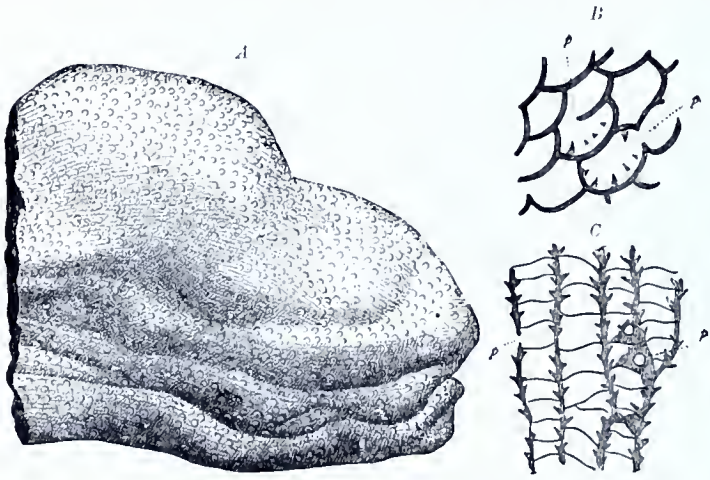


Fig. 177.

A, *Alveolites suborbicularis*, Lam. Middle Devonian; Gerolstein, Eifel. Natural size. *B* and *C*, *Alveolites Labechei*, E. and H. Silurian (Wenlock); Ironbridge, England. Tangential and vertical sections, $^{10}/_{1}$ (after Nicholson).

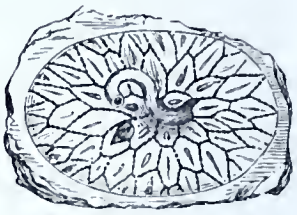


Fig. 178.

Pleurodictyum problematicum, Goldf. Lower Devonian; Coblenz. Natural size. Vermiform foreign body in the centre.

or rows of spinules, sometimes but a single row present. Mural pores of large size, irregularly distributed. Very common in Silurian and Devonian.

Cladopora, Hall. *Coenites*, Eichw. Silurian and Devonian.

Pleurodictyum, Goldf. (Fig. 178). Corallum depressed, discoidal, circular, or elliptical in contour, lower surface covered with concentrically striated

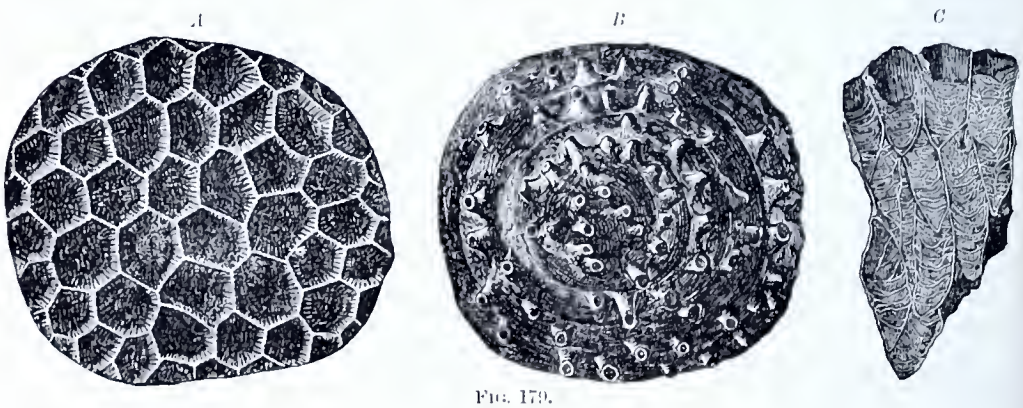


Fig. 179.

Michelinia favosa, de Kon. Carboniferous Limestone; Tournay, Belgium. *A*, Corallum from above. *B*, Lower surface with radiciform epithecal processes. *C*, Vertical section (after Gaudry).

epitheca, and frequently with foreign vermiform body occupying centre of the base. Corallites small, polygonal, contracted inferiorly so as to become funnel-shaped. Septa represented by faint marginal ridges, or obsolete. Walls pierced by irregularly distributed mural pores. Tabulae scanty. Devonian. *P. problematicum*, Goldfuss, is tolerably abundant in the Lower Devonian "Spirifera sandstone" of the Eifel, but is only known in the form of casts.

In these the walls of the corallites are represented by narrow fissures which are bridged across by transverse rods, while the visceral chamber is filled up with sandstone. *P. stylopora*, Eaton, from the Hamilton Group of North America, is a closely related species, and also possesses the vermiform body.

Michelinia, de Kon. (Fig. 179). Discoidal or hemispherical coralla, often of considerable size, and covered on the under surface with concentrically striated epitheca, which frequently develops hollow radiciform processes. Corallites polygonal, rather large. Septa represented by numerous longitudinal striae or ridges; mural pores irregularly distributed; tabulae very numerous, oblique or curved, incompletely developed, and usually filling the visceral chamber with loose vesicular tissue. Devonian and Carboniferous. *M. favosa*, de Kon., extraordinarily profuse in Carboniferous Limestone of Belgium.

Family 2. **Auloporidae.** Nich. (*Tubulosa*, Milne-Edwards and Haime).

Creeping, branching, or reticulated tubular coralla, composed of cylindrical, beaker, or trumpet-shaped corallites, with thick, imperforate, wrinkled walls. Septa represented by faint marginal striae; tabulae moderately numerous or wanting. Reproduction by basal or lateral gemmation. Ordovician to Carboniferous.

Aulopora, Goldf. (Fig. 180). All the corallites of the prostrate corallum are attached by the whole of the lower surface to some foreign object (*Alveolites*, other corals, or mollusks). Tabulae more or less curved; reproduction by basal gemmation. Ordovician to Carboniferous.

Cladochonus, M'Coy (*Pyrgia*, E. and H.) Corallum branching, attached only at isolated points, and composed of funnel-shaped corallites without tabulae and septa. Reproduction by lateral gemmation. Carboniferous.

Romingeria, Nich. (*Quenstedtia*, Rom.) Spreading, semi-erect, bushy coralla, only basally attached, and with cylindrical corallites increasing by lateral gemmation. Tabulae moderately numerous, horizontal. Silurian and Devonian.

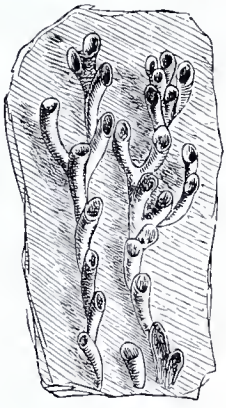


FIG. 180.

Aulopora tubaeformis, Goldf. Devonian; Gerolstein, Eifel. Natural size (after Goldfuss).

Family 3. **Syringoporidae.** Milne-Edwards and Haime.

FIG. 181.

Syringopora ramulosa, Goldf. Carboniferous Limestone; Regnitzlosau, Fichtelgebirge. Natural size.

Fasciculate coralla composed of cylindrical corallites, united at intervals along the sides by hollow connecting processes or by horizontal expansions. Walls thick, wrinkled; septa faintly developed, represented by delicate ridges or longitudinal rows of spinules; tabulae numerously developed, usually irregularly funnel-shaped. Reproduction by basal gemmation or by buds arising from the connecting processes and horizontal expansions. Ordovician to Carboniferous; maximum in Devonian and Carboniferous.

Syringopora, Goldf. (Fig. 181). Fasciculate coralla, often attaining considerable size, and composed of cylindrical, thin-walled, somewhat flexuose corallites; the latter communicate by means of hollow, cylindrical, connecting processes. Septa rudimentary; tabulae funnel-shaped.

Corallum commencing with prostrate basal network similar to *Aulopora*. Numerous species ranging from Silurian to Carboniferous.

Chonostegites, E. and H. Corallum massive; cylindrical corallites connected by horizontal, hollow, laminar expansions into which the endothecal tissues are directly continued; tabulae oblique, cystoid. Devonian.

Fig. 182.

Halysites catenularia, Lin. sp. Silurian; Gottland. Natural size.

Thecostegites, E. and H. Corallum encrusting; corallites short, cylindrical, and connected by thick horizontal plates. Tabulae approximately horizontal; septa twelve in number, represented by marginal ridges. Devonian.

Family 4. **Halysitidae.** Milne-Edwards and Haime. Chain corals.

Corallum composed of long, cylindrical, laterally compressed corallites, which are joined to one another only along the more constricted edges, and form free, vertical, intersecting, and anastomosing laminae. Wall thick, covered on free sides by wrinkled epitheca; tabulae numerous, horizontal, or concave; septa represented by vertical ridges or rows of spines, in cycles of twelve, sometimes entirely absent. Increase by stolonal gemmation.

The single genus *Halysites*, Fischer (*Cateniporu*, Lam.), (Fig. 182), comprises two groups of species; those in which the corallum is composed throughout of corallites of equal size (*H. escharoides*, Lam. sp.), and others in which any two of the larger corallites are separated by the intervention of a single smaller, closely tabulate tube (*H. catenularia*, Lin.) Ordovician and Silurian; maximum in Silurian.

Family 5. **Chaetetidae.** Milne-Edwards and Haime.

Massive coralla, composed of fine, subequal, tubiform corallites, contiguous on all sides. Calices rather irregular in shape, one diameter slightly greater than the other. Walls thoroughly amalgamated, common to adjacent corallites, imperforate, apparently composed of closely arranged, ankylosed vertical columns, which terminate at the surface in hollow prominences. Septa absent, but one or two tooth-like projections often observable in sections. Tabulae horizontal, remote or abundant.

All the forms belonging to this family are extinct, and occur chiefly in the Ordovician, Silurian, Devonian, and Carboniferous systems; but they are also found sporadically in the Trias, Jurassic, and Cretaceous. They are important as being largely concerned in the formation of Palaeozoic coral reefs, especially during the Ordovician. Milne-Edwards and Haime regarded them as Anthozoans, Rominger and Lindström as Bryozoans; while Dybowski, though admitting their resemblance to certain Bryozoans, emphasised their affinities with the *Favositidae*. By Nicholson they were assigned to the *Octocoralla*, for the reason that the corallites frequently exhibit a dimorphous character the same as in *Heliolites* and *Heliopora*, besides agreeing in their microscopic structure with *Heliolites*; while in addition they possess well-developed tabulae and imperforate walls, and increase by intermural gemmation or by fission. Nevertheless, their resemblance to certain of the cyclostomatous Bryozoans (*Heteropora*) is fully recognised by Nicholson, and insisted on by Ulrich.

Chaetetes, Fischer (Figs. 183, 184). Corallites long, thin-walled, prismatic,

polygonal, all of one kind, and multiplying by fission. Uncompleted fission of the tubes often indicated in section by tooth-like projection extending into visceral chamber. Walls structureless, without dark median line; tabulae complete, remote. Very abundant in Carboniferous Limestone; found also in Lias and Upper Jurassic. *C. radians*, Fisch., is an important rock-builder in the Russian Carboniferous Limestone, especially in the vicinity of Moscow.

Fig. 184.

Chaetetes radians, Fischer. Carboniferous Limestone; Moscow, Russia. Portion of longitudinally fractured corallum, natural size.

Pseudochaetetes, Haug; Upper Jurassic. *P. polyporus*, Quenst. sp.

Monticulipora, d'Orb. (emend. Nich.), (Figs. 185-187). Massive, tuberous, hemispherical, discoidal, ramose, or encrusting coralla of extremely variable form and size, and composed of numerous, fine, tubular corallites, usually of two series, the walls of which are imperforate and closely approximated to one another, but are not amalgamated. Multiplication by intermural gemmation, more rarely by fission. Tabulae horizontal, and either complete, extending entirely across the visceral chamber, or incomplete; in the latter case the spaces where tabulae are not developed are filled with large

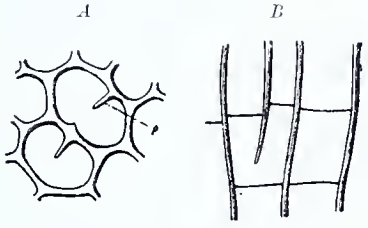


Fig. 183.

Chaetetes septosus, Flem. Carboniferous Limestone; England. *A*, Transverse section parallel to upper surface. *B*, Vertical section, both enlarged; *p*, Projecting spines representing uncompleted fission (after Nicholson).

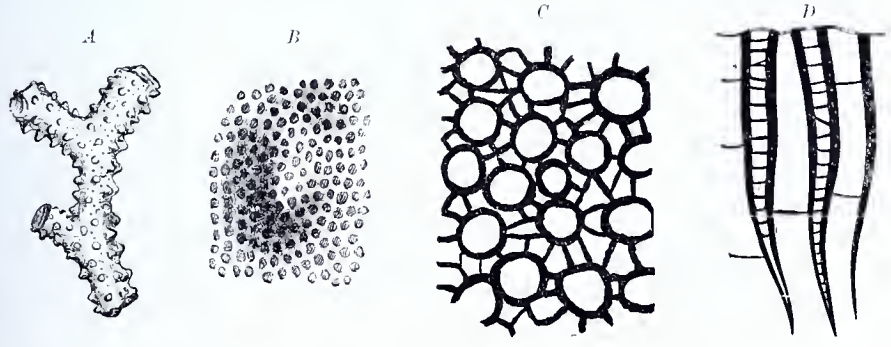


Fig. 185.

Monticulipora (*Heterotrypa*) *ramosa*, E. and H. Ordovician (Cincinnati Group); Cincinnati, Ohio. *A*, Corallum, natural size. *B*, Surface slightly magnified. *C*, Tangential section, parallel to external surface, $^{20}/_{1}$. *D*, Vertical section, $^{20}/_{1}$. (*C* and *D* after Nicholson.)

cystoid calcareous plates. The walls differ from those of *Chaetetes* in that they are composed of two distinct lamellae separated by a dark or light median line, and are sometimes thickened by deposits of carbonate of lime. The corallites are polygonal or round in contour, and, as a rule, two series are distinguishable; a series of larger tubes with remotely situated tabulae, and another series of more or less numerous interstitial tubes, which are smaller and more closely tabulate than the former. The larger tubes (*autopores*) are often surrounded on all sides

by the smaller (*mesopores*), and hence are completely separated from one another. Occasionally, in addition to the preceding, a further series of tubes called *acanthopores* occur, which are thick-walled and form small tubercles on the surface. Extraordinarily abundant in Ordovician and Silurian, particularly the former; rarer in Devonian and Triassic.

Nicholson compares the mesopores of *Monticulipora* with the siphonopores of *Heliopora*, and supposes the corallum to have been inhabited by dimorphous

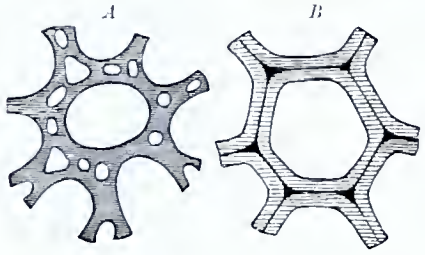


Fig. 186.

Enlarged tangential sections parallel to external surface. *A*, *Monticulipora* (*Heterotrypa*) *pulchella*, E. and H. *B*, *M.* (*Heterotrypa*) *ramosa*, E. and H. (after Nicholson).

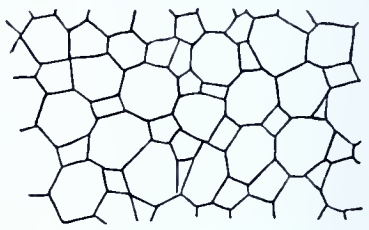


Fig. 187.

Monticulipora (*Diplotrypa*) *Petropolitana*, Pand. Ordovician; St. Petersburg. Enlarged tangential section parallel to external surface (after Dybowski).

polyps. F. Roemer holds the smaller tubes for immature corallites formed by budding. The following sub-genera are recognised by Nicholson:—

a. *Heterotrypa*, Nich. (Figs. 185, 186). Corallites of two kinds, the larger ones sub-polygonal, and separated by a single row of mesopores. Walls

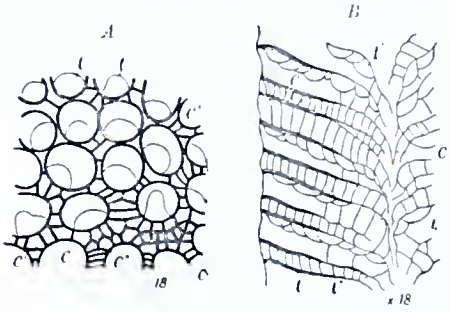


Fig. 188.

Prasopora Selwynii, Nich. Ordovician; Ontario. *A*, Tangential section parallel to exterior. *B*, Vertical section, enlarged. *C*, Autopores; *t*, Tabulae; *t'*, Cystoid tabulae (after Nicholson).

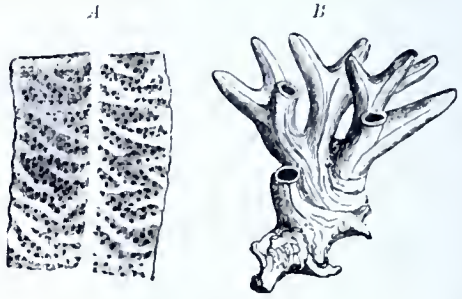


Fig. 189.

Neuropora angulosa, Goldf. sp. Upper Jurassic; Oerlingen, near Ulm. *A*, Portion of external surface enlarged. *B*, Corallum, natural size.

thickened towards mouths of tubes; tabulae horizontal; acanthopores generally present.

b. *Monotrypa*, Nich. Corallites all similar, or of two kinds, not conspicuously different in size, and usually polygonal and thin-walled. Ordovician to Devonian, also Triassic. *M. Recubariensis*, Schaur. sp.

c. *Diplotrypa*, Nich. (*Dianulites*, Eich.), (Fig. 187). Corallites of two kinds, uniformly thin-walled; the autopores aggregated into clusters or monticules, but also scattered with the mesopores throughout the colony. Ordovician.

d. *Prasopora*, Nich. (Fig. 188). Corallites of two kinds, uniformly thin-walled; mesopores with numerous horizontal tabulae, autopores with incomplete and cystoid tabulae. Ordovician and Devonian.

e. *Peronopora*, Nich. Like the preceding, but thick-walled.

Stenopora, Lonsd. Branching or lobate coralla composed of fine tubular corallites radiating outwards and becoming reflexed. Walls thickened by annular deposits of stereoplasma; tabulae scanty. Abundant in Carboniferous and Zechstein.

Geinitzella, Waag. and Wentz. Like the preceding, but with walls only slightly thickened. Carboniferous to Zechstein.

? *Neuropora*, Bronn. (*Chrysaora*, Lamx.), (Fig. 189). Ramose or tuberous coralla, composed of long, polygonal tubes, nearly uniform in size, and with mouths separated into groups by elevated, non-tubular ridges; tabulae numerous. Jurassic and Cretaceous.

Family 6. **Fistuliporidae.** Waagen and Wentzel.

Encrusting, massive, or branching coralla, composed of two series of fine tubiform corallites. Walls compact; tabulae horizontal; septa wanting. Autopores multiplying by coenenchymal gemmation, mesopores by fission. Silurian to Zechstein.

The *Fistuliporidae* resemble the *Helioporidae* in a number of particulars, especially as regards the coenenchymal gemmation of the autopores. Waagen assigns them to the vicinity of the *Helioporidae*, while Nicholson regards them as a sub-family of the *Monticuliporidae*.

Fistulipora, M'Coy. Corallum composed of two series of tubiform corallites; autopores round or sub-triangular in contour, and embedded in a coenenchyma constituted of the smaller mesopores. The latter are much more closely tabulate than the autopores, and give the coenenchyma a vesicular, multicellular appearance. Walls of the autopores are thickened on one side, and frequently provided with two septa-like processes. Common in Devonian, Carboniferous, and Permian.

Callopora, Hall; *Prasopora*, Nich. Ordovician and Silurian. *Labechia*, E. and H., occurring in the Ordovician and Silurian, probably also belongs here.

Geological Range of the Tabulata.

With but few exceptions, the *Tabulata* are restricted to the Palaeozoic formations, and from the Ordovician to the Carboniferous periods inclusive are prominently concerned along with the *Tetracoralla* and *Hydrozoa* (*Stromatoporidae*) in the building of coral reefs. Of the six families composing the *Tabulata*, the *Halysitidae* alone are confined to the Silurian; the rest are all more or less plentiful from the Ordovician to the Carboniferous; while the *Fistuliporidae* persist as late as the Zechstein, and the *Chaetetidae* range from the Ordovician to the Cretaceous.

Sub-Class 3. OCTOCORALLA. Haeckel.

(*Octactinia*, Ehrenberg; *Alcyonaria*, Milne-Edwards.)

Composite colonies, rarely simple polyps, the individuals provided with eight mesenterial folds and eight broad, pinnately fringed, or plumose tentacles, which form a single cycle about the mouth.

Hard skeletal elements are very generally developed in the *Octocoralla*, being absent in comparatively few forms, and are remarkable for their manifold

variety; they occur either detached in the ectoderm and mesoderm, or are closely packed together at the base to form a horny or calcareous axis (*sclerobasis*), about which the polyps are distributed. Sometimes the calcareous bodies (*sclerodermites*) form compact tubes which are periodically partitioned off into storeys with the upward growth of the animal. Reproduction is accomplished either sexually or asexually by basal or lateral gemmation, rarely by fission.

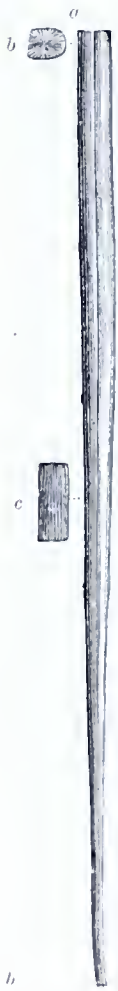


Fig. 190.

Graphularia desertorum, Zitt. Nummulitic limestone (Eocene); Farafreh, Libyan Desert. *a*, Axis, natural size; *b*, *b'*, Cross-sections; *c*, Striated surface, enlarged.

Only the calcareous parts are known in the fossil state, such as the solid axes, detached skeletal elements, tubes, and composite coralla; the horny structures are totally destroyed during fossilisation. The *Octocoralla* make their appearance in the Ordovician, but belong only exceptionally to the more common fossils.

Family 1. **Alcyonidae.** Milne-Edwards and Haime.

Fixed, fleshy, lobate, or ramose polyp stocks (very rarely simple individuals), with echinulate or spicular calcareous bodies (sclerodermites) occurring detached in the soft parts.

Isolated sclerodermites readily escape observation, owing to their minute size and fragile constitution. They have been detected as yet only by Počta[1] in the Upper Cretaceous strata near Laun, Bohemia.

Family 2. **Pennatulidae.** Milne-Edwards and Haime.

Polyp stocks with base embedded in sand or mud, and with horny or calcareous sclerobase; polyps dimorphic.

Slender, round, or quadrate calcareous axes referable to the *Pennatulidae* have been detected with certainty only in the Trias (*Prographularia*, Frech.), Cretaceous (*Paronaria*, Cuv.; *Pennatulites* and *Palaeosceptron*, Cocchi; *Glyptosceptron*, Böhm), and Tertiary (*Graphularia*, E. and H.), (Fig. 190).

Family 3. **Gorgonidae.** Milne-Edwards and Haime.

Fixed, branching, or fan-shaped colonies, with horny or calcareous solid sclerobase, or with jointed axis composed of alternating horny and calcareous segments.

All the genera possessing horny, flexible axes (*Gorgonia*, *Rhipidogorgia*, etc.) are perishable. Detached remains referable to *Primnoa*, *Gorgonella*, and *Virgularia*, the axes of which are composed of both horny and calcareous layers, have been described from the Tertiary. In the genus *Isis* the axis consists of cylindrical, calcareous segments alternating with horny connecting joints. It is found fossil in the Tertiary, and has been reported also from the Cretaceous. The genus *Moltkia*, occurring in the Upper Cretaceous, has cylindrical joints which are pitted with slight depressions indicating the position of branches. In the red or gem coral (*Corallium*, Lin.) the axis is built up of spiniform sclerites, which are united

[1] *Počta. Philipp.* Sitzungsberichte der Wiener Akad. der Wissensch., Bd. 92. Jahrg. 1885.

by a fibro-crystalline calcareous matrix impregnated with organic matter. It is found but rarely in the fossil state, but is known from the Cretaceous and Tertiary.

Family 4. **Tubiporidae.** Milne-Edwards and Haime.

Coralla composed of red-coloured parallel calcareous tubes connected by horizontal plates.

The cylindrical tubes of the recent Organ-pipe Coral (*Tubipora*) are composed of spiniform sclerites, which are united with one another directly in such manner as to enclose small hollow spaces appearing superficially as pores. The connecting horizontal plates or floors are traversed by canals which communicate with the visceral chambers of the tubes by means of numerous round openings; new corallites are budded from their upper surfaces. Unknown in fossil state.

Family 5. **Helioporidae.** Moseley.

Calcareous coralla, composed of two series of tubiform corallites; the larger tubes (autopores) are embedded in a strongly developed coenenchyma made up of smaller tubes (siphonopores). Both autopores and siphonopores are closely tabulate; the autopores are provided with ridge-like pseudosepta, which, however, do not correspond numerically with the tentacles.

The affinities of the *Helioporidae* with the *Octocoralla* were first pointed out by Moseley.[1] The larger polyps inhabit the autopores, and are furnished with eight mesenterial folds and a crown of eight tentacles; while the smaller polyps, which are without either tentacles or sexual organs, are lodged in the siphonopores. The skeleton is composed of calcareous trabeculae, the same as in the *Hexacoralla*, from whose centres of calcification radial fibres extend outwards in caespitose fashion. The siphonopores multiply by intermural gemmation, while the autopores are formed by the coalescence and fusion of a number of the siphonopores.

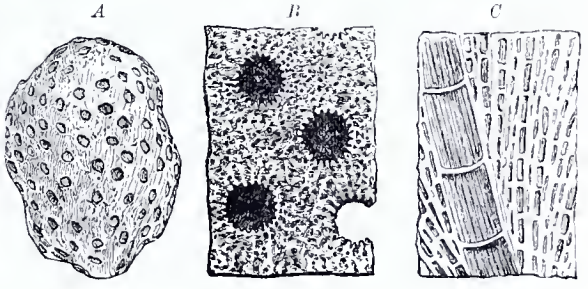


Fig. 191.

Heliopora Partschi, Reuss sp. Upper Cretaceous; St. Gilgen on Wolfgangsee, Salzkammergut. *A*, Corallum, natural size. *B*, Portion of surface, enlarged. *C*, *Polytremacis Blainvilleana*, Reuss. Upper Cretaceous; Gosau, Salzkammergut. Vertical section, enlarged.

Heliopora, Blainv. (Fig. 191, *A*, *B*). Corallum massive or ramose; autopores with 12-25 slightly developed pseudosepta, and embedded in a coenenchyma made up of smaller siphonopores; the latter are more closely tabulate than the autopores. Cretaceous to Recent.

Polytremacis, d'Orb. (Fig. 191, *C*). Like *Heliopora*, but pseudosepta much more strongly developed, sometimes reaching nearly to the centre. Cretaceous.

Certain Palaeozoic corals (*Heliolitidae*) exhibiting characters very similar to *Heliopora* are assigned to the same vicinity with the latter by Moseley, Nicholson, and other authors. Like *Heliopora*, the corallum in these forms is massive, and consists of larger tubes embedded in a coenenchyma formed of

[1] *Moseley, H. N.*, Philosophical Transactions, Royal Society, vol. 166, 1877.

smaller tubes. Both series of corallites are provided with numerous horizontal tabulae; and, as in *Heliopora*, the autopores are produced by the coalescence of a number of adjoining coenenchymal tubes. In the *Heliolitidae*, however, twelve well-developed septa are uniformly present. The walls of the corallites are composed of homogeneous, compact, calcareous matter, and exhibit the same

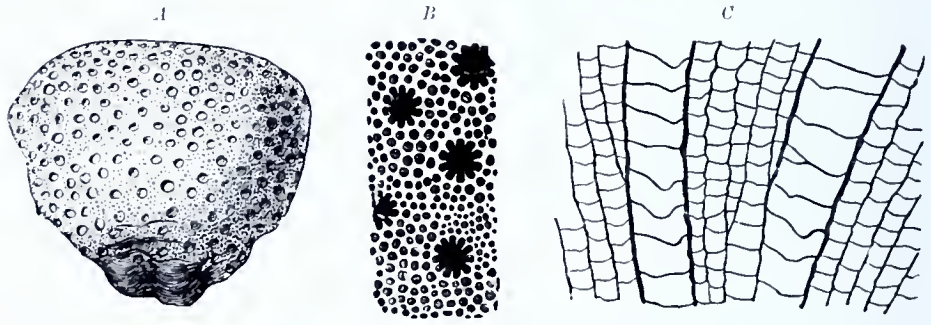


FIG. 192.

Heliolites porosa, Goldfuss. Devonian; Eifel. *A*, Corallum, natural size. *B*, Portion of outer surface enlarged. *C*, Longitudinal section, enlarged.

histological structure as the *Favositidae* and *Chaetetidae*. Owing to these anomalies the systematic position of the *Heliolitidae* remains uncertain.

Heliolites, Dana (Fig. 192). Corallum massive, nodular, or ramose. Autopores with twelve more or less strongly developed pseudosepta, though occasionally represented by rows of spinules, and frequently with central columella. Siphonopores without septa, and multiplying by fission or intermural gemmation. Abundant from Ordovician to Devonian.

Plasmopora, E. and H. Like *Heliolites*, but having walls of the siphonopores incomplete, and tabulae of contiguous tubes fused together so as to form a vesicular tissue. Ordovician to Devonian.

Class 2. HYDROZOA. Huxley. Hydroids and Medusae.[1]

Sessile or free-swimming polyps or polyp stocks, without oesophageal tube, and with simple gastrovascular cavity not divided into radial pouches.

The Hydrozoans are organisms which rarely secrete hard parts, and hence are ill-adapted for preservation in the fossil state. The ramifying polyp stocks are usually inferior in size to those of the *Anthozoa*, and possess always a simpler structure; dimorphism or polymorphism is, however, exhibited by the different individuals, some of which perform solely vegetative, and others only locomotive functions. Of great interest is the prevailing alternation of generations, in which process fixed polyp stocks give rise to a generation of free-swimming Medusae, the eggs of which develop in turn into polyps.

The *Hydrozoa* are all aquatic, and with few exceptions are inhabitants of the sea. They are commonly divided into the two following sub-classes:—*Hydromedusae* and *Acalephae*.

[1] *Huxley, T. H.*, The Oceanic Hydrozoa. London, 1859.—*Agassiz, A.*, North American Acalephae (Ill. Ca'. Museum Comp. Zool. Cambridge, U.), 1865.—*Hincks, T.*, Natural History of the British Hydroid Zoophytes, London, 1868.—*Claus, C.*, Untersuchungen über die Organisation, etc., der Medusen. Leipzic, 1883. Cf. also references on pp. 109, 114, and 121.

Sub-Class 1. HYDROMEDUSAE. Vogt.[1]

Sessile or free-swimming, usually branching colonies, with dimorphic, nutritive, and reproductive polyps; the latter frequently become liberated in the form of small, free-swimming Medusae, with non-lobate umbrellas composed of a hyaline, gelatinous substance.

Six orders of *Hydromedusae* are recognised—*Hydrariae*, *Hydrocorallinae*, *Tubulariae*, *Campanulariae*, *Trachymedusae*, and *Siphonophorae*. But of these only the *Hydrocorallinae*, *Tubulariae*, and *Campanulariae* secrete durable, calcareous, or chitinous structures.

Order 2. HYDROCORALLINAE. Moseley.[2]

Naked polyps secreting at the base a dense calcareous skeleton, traversed at intervals by two series of vertical tubes, into which the dimorphic zoöids can be retracted.

The *Hydrocorallinae* comprise the two recent groups *Milleporidae* and *Stylasteridae*, which were universally regarded as true corals until Louis Agassiz and Moseley proved their relationship to the *Hydrozoa*.

Millepora, Lin. (Fig. 193). Massive, foliately expanded, encrusting, or branching polyparia (*coenosteum*), often attaining considerable size. Upper surface punctured by round openings of the larger tubes (*gastropores*), between which are the mouths of numerous smaller tubes (*dactylopores*). The skeleton is composed of a network of anastomosing calcareous fibres, traversed by a system of tortuous canals. The gastropores lodge the larger, nutritive polyps, and the dactylopores the smaller, food-procuring zoöids; the latter have no mouth, but are provided with short, clavate tentacles on their sides, and their tubes communicate with the vermiform canals. Zoöidal tubes tabulate, but non-septate. The genus is an important reef-builder of the present day, but occurs only sparsely in the fossil state. Earliest known forms appear in the Eocene.

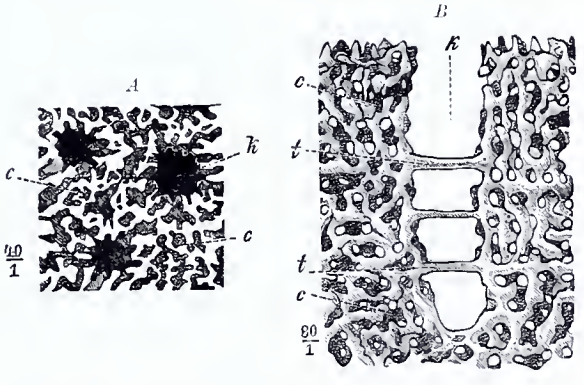


Fig. 193.

Millepora nodosa, Esp. Recent. *A*, Upper surface of coenosteum, showing gastropores, *k*, and dactylopores, *c*, $^{40}/_{1}$. *B*, Vertical section, *k*, gastropores with tabulae, *t*; *c*, Vermiform canals communicating with dactylopores, $^{80}/_{1}$ (after Steinmann).

Stylaster, Gray. Branching polyparia composed of a network of fibrous, rose-coloured coenenchyma, in which are situated calicular depressions that are

[1] *Allman, J. G.*, Monograph of the Gymnoblastic or Tubularian Hydroids; Ray Society, 1871-72.—*Steinmann, G.*, Ueber fossile Hydrozoen aus der Familie der Coryniden (Palaeontographica, Bd. XXV.), 1877.—Ueber triasische Hydrozoen vom östlichen Balkan (Sitzungsber. Wiener Akad. math. phys. Classe, Bd. CII.), 1893.—*Canavari, M.*, Idrozoi Titoniani appartenanti alla Famiglia delle Ellipsactinidi (Mem. Comitato Geol. vol. IV.), 1893.—*Nicholson, H. A.*, Monograph of the British Stromatoporoids (Palaeontographical Society), 1886-92.—*Bargatzki, A.*, Die Stromatoporen des rheinischen Devons. Bonn, 1881.

[2] *Moseley, H. N.*, Philosophical Transactions Royal Society, vol. 167, 1878.

provided with pseudosepta and columellae, and communicate with the zoöid tubes and vermiform canals. Recent, and occurring sparsely in the Tertiary.

Order 3. TUBULARIAE. Allman.

Polyp stocks which are either naked or covered with chitinous outer layer (periderm). Both the polypoid nutritive zoöids, and also the medusoid reproductive animals are without cup-shaped hydrothecae surrounding the polyp head. A chitinous or calcareous skeleton (hydrophyton) is frequently secreted at the base.

Hydractinia, v. Bened. (Fig. 194). Hydrophyton in the form of encrusting, chitinous, rarely calcareous expansion, frequently investing gastropod shells. The crust consists of successive, slightly separated, horizontal laminae, which are supported by numerous vertical rods or columns (*radial pillars*). The surface is covered with projecting hollow spines and tubercles, and is also traversed by shallow, branching grooves (*astrorhizae*). Interlaminar spaces communicating with the surface by means of rounded tubes. Tertiary and Recent.

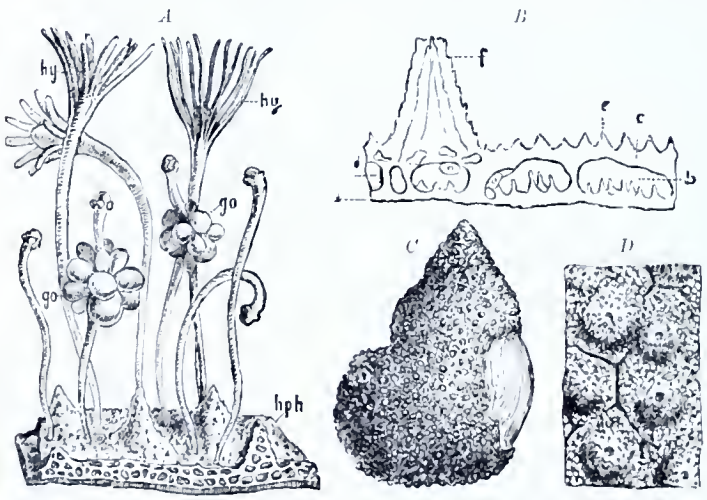


FIG. 194.

* *A, Hydractinia echinata*, Flem. Recent; North Sea. Portion of parasitic colony, greatly enlarged; *hy*, Polyps (hydranths); *go*, Generative buds (gonophores); *hph*, Hydrophyton adherent to shell of *Buccinium undatum*, and showing reticulated structure in vertical section. *B, Hydractinia calcarea*, Cart. Vertical section of hydrophyton, greatly enlarged (after Carter); *a*, Primary basal lamella; *b*, Interlaminar space; *c*, Second lamella; *d*, Radial pillars between the lamellae; *e, f*, Tubercles and spines projecting on upper surface. *C, Hydractinia pliocaena*, Allm. Pliocene; Asti, Italy. Hydrophyton encrusting on *Nassa* shell (natural size). *D*, Portion of magnified surface of the latter, showing branching grooves and wart-like tubercles.

Ellipsactinia, Steinm. Hydrophyton irregularly ellipsoidal, composed of thick, concentric, slightly separated, calcareous lamellae, which are united by sparsely distributed vertical columns. Lamellae are formed by the anastomosis of exceedingly delicate calcareous fibres, punctured by numerous fine radial tubes, and furnished on both sides with pits, tubercles, and branching furrows. Upper Jurassic (Tithonian); Alps, Carpathians, and Apennines.

Sphaeractinia, Steinm. Like the preceding, but composed of thin, widely separated lamellae, which are supported by numerous radial pillars. Centre frequently occupied by a foreign body. Upper Jurassic (Tithonian).

? *Loftusia*, Brady (Fig. 195). Ellipsoidal or fusiform bodies, composed of thin, concentric, or spirally rolled calcareous lamellae. Interlaminar spaces wide, intersected by numerous radial pillars, and often secondarily filled with calcareous mud. Eocene; Persia.

Parkeria, Carp. Globular or walnut-shaped organisms with nodulated exterior, and composed of rather thick, concentric, calcareous lamellae. Interlaminar spaces divided into chamberlets by stout radial pillars, which usually

extend continuously through a number of lamellae. Both lamellae and pillars consist of minutely tubulated tissue, the tubules of which are radial in arrangement. Centre frequently occupied by a foreign body. Cambridge Greensand (Cenomanian).

The genera *Parkeria* and *Loftusia* were originally described as agglutinated Foraminifera; but they are manifestly very closely allied to *Ellipsactinia* and *Sphaeractinia*.

Porosphaera, Steinm. (Fig. 196). Globular masses of the size of peas or hazel-nuts, frequently growing around some foreign body, and composed of anastomosing calcareous fibres which are penetrated by numerous radial tubules; the latter open on the surface in the form of large pores, around which radial or stellate furrows (*astrorhizae*) are sometimes grouped. Upper Cretaceous.

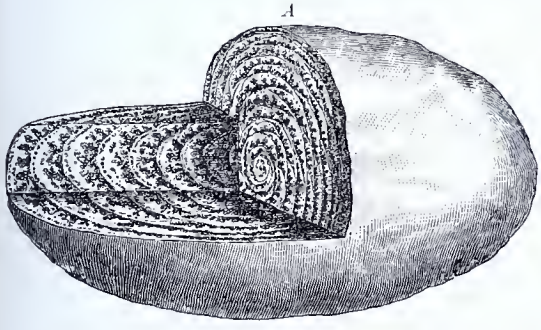


Fig. 195.

Loftusia Persica, Brady. Eocene; Persia. *A*, Specimen cut open to show general structure, natural size (after Brady). *B*, Section showing two lamellae and interlaminar filling, greatly enlarged.

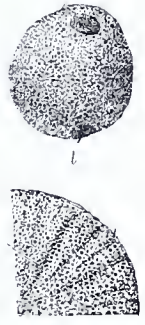


Fig. 196.

Porosphaera globularis, Phill. sp. Upper Cretaceous; Rügen. *A*, Skeleton, natural size; *l*, Cavity originally occupied by foreign body. *B*, Transverse section showing radial tubes of gastropores, 2/1 (after Steinmann).

Stoliczkaria, Duncan. Trias; Karakoram and Balkan Mountains.

Heterastridium, Reuss. (*Syringosphaeria*, Duncan). Spheroidal, nodular bodies of considerable size, composed of slender, anastomosing, and more or less distinctly radial calcareous fibres. Skeleton comparatively dense, but perforated by two series of zoöidal tubes appearing superficially as pores. The apertures of the larger tubes are round, those of the smaller stellate, and are surrounded by radial furrows. Alpine Trias.

Appendix to the Hydrocorallinae and Tubulariae.

Stromatoporoidea. Nicholson and Murie.

Closely allied to the *Hydrocorallinae* and *Hydractinia* are the extinct *Stromatoporoidea*, which combine in many respects the characters pertaining to both of the above-named groups, but whose exact position in the zoological system remains as yet uncertain. During the Palaeozoic era, to which they are confined, the Stromatoporoids were important geological agents, whole beds of limestone being often essentially constituted of their remains. In the Mesozoic era they are replaced by very closely allied forms of *Hydractinia*, which in all probability represent their immediate descendants.

The Stromatoporoids secrete hemispherical, globular, nodular, or horizontally expanded skeletons, which are sometimes encrusting, sometimes attached by a short basal peduncle, and are covered on the under side with concentrically

wrinkled epitheca, while the apertures for the emission of the polyps are situated on the upper surface. The general tissue of the coenosteum is composed of numerous, concentric, undulating, calcareous layers or *laminae*, which are separated by narrower or wider interlaminar spaces, but are at the same time connected by numerous vertical rods (*radial pillars*). The pillars as well as the laminae are traversed, as a rule, by minute, irregularly directed canaliculi. In some genera the coenosteum is provided with vertical tabulate tubes, which most probably served for the reception of the polyps, as in the genus *Millepora*; but in many instances they are wanting. The surfaces of the laminae typically exhibit pores and small tubercles, and frequently also shallow stellate furrows (*astrorhizae*), which radiate outwards from numerous centres. Sometimes the laminae consist merely of a loose network of horizontal calcareous fibres.

Goldfuss at first held the Stromatoporoids occurring so profusely in the Eifel for corals (*Millepora*), and subsequently for sponge-like zoophytes; while von Rosen considered them as horny sponges that had become secondarily calcified. Sandberger and F. Roemer assigned them to the Bryozoans; Dawson to the Foraminifera; Sollas to the silicious sponges (*Hexactinellida*); and Salter to the calcareous sponges, whose example Nicholson also followed. Lindström, Carter, and Steinmann subsequently pointed out their relations to *Hydractinia* and *Millepora*: and Nicholson and Murie now regard them as constituting an independent group of extinct Hydrozoans allied to *Hydractinia* on the one hand (*Actinostromidae*), and *Millepora* on the other (*Stromatoporidae* and *Idiostromidae*).

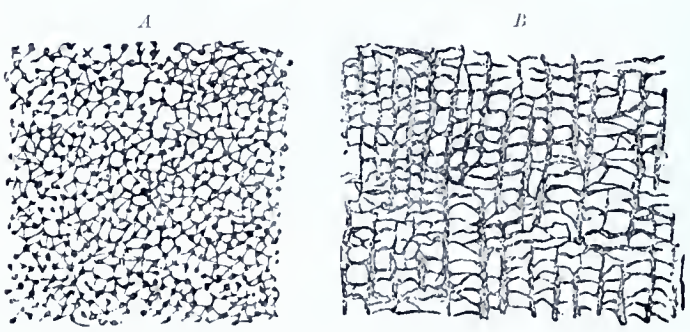


Fig. 197.

Actinostroma intertextum, Nich. Silurian (Wenlock); Shropshire. *A*, Tangential section showing radial pillars and reticulated structure of concentric laminae. *B*, Vertical section, showing formation of laminae out of processes given off horizontally by radial pillars, $^{12}/_{1}$ (after Nicholson).

Actinostroma, Nich. (Fig. 197). Skeleton having vertical or radial pillars disposed at tolerably regular intervals, and extending continuously through all or at least a considerable number of laminae; in vertical sections, accordingly, exhibiting a quadrate meshwork. The laminae consist of an anastomosing network of calcareous fibres, generally having a porous structure; their surfaces are covered with projecting granules or tubercles, which represent the free upper ends of the vertical pillars. Rare in Silurian, but very abundant in Devonian of the Eifel, England, and North America. *A. clathratum*, Nich. (= *Stromatopora concentrica*, pp., Goldf.)

Clathrodictyon, Nich. Like the preceding, but with radial pillars extending only between the upper and lower surfaces of successive laminae. Characteristic of Silurian; rare in Devonian.

Stromatopora, Goldf. emend. Nich. (*Pachystroma*, Nich. and Murie), (Fig. 198). Radial pillars uniting with the thick concentric strata or latilaminae to form a finely reticulated tissue, in which tabulate zoöidal tubes are sparsely distributed. Plentiful in Devonian; less common in Silurian.

Caunopora, Lonsd. (Fig. 199), and *Diapora*, Bargat., are Stromatoporoids which are indistinguishable from other species except by the presence of numerous definitely walled tubes penetrating the coenosteum at closer or

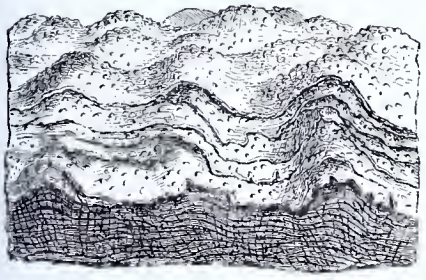


Fig. 198.

Stromatopora tuberculata, Nich. Devonian (Corniferous limestone); Jarvis, Ontario. Natural size (after Nicholson).

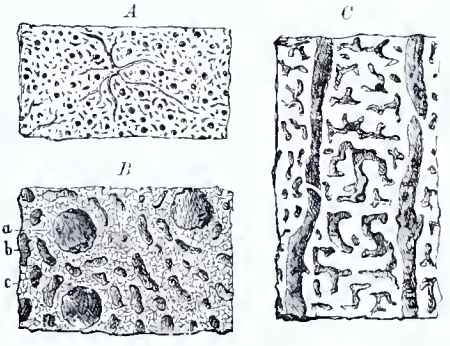


Fig. 199.

Caunopora placenta, Phill. Devonian; Torquay, Devonshire. *A*, Tangential section, natural size. *B*, The same, highly magnified; *a*, Vertical "Caunopora tube"; *b*, Canal partially cut into; *c*, Calcareous fibres traversed by delicate ramifying canaliculi. *C*, Vertical section, highly magnified.

remoter intervals. The tubes are often thick-walled, are furnished with horizontal or funnel-shaped tabulae, and occasionally with septal spines; in many cases they evidently represent the corallites of *Aulopora* and *Syringopora* colonies, which have become enveloped, but have continued to live commensally within the tissues of the Stromatoporoid. In other cases, however, the tubes appear to have been formed by true Stromatoporoid polyps. Devonian.

Hermatostroma, Nich. (Fig. 200). Massive or foliaceous skeletons, composed of thick parallel latilaminae, connected by vertical pillars; pillars often running continuously through several concentric laminae. Both pillars and laminae exhibit a dark median line when viewed in cross-section, indicating either the presence of axial canals or composition out of two lamellae. Devonian.

Fig. 200.

Hermatostroma, sp. Devonian; Torquay, Devonshire. *a*, Horizontal lamina composed of two slightly separated lamellae; *b*, Interlaminar chamberlet; *c*, Radial pillar traversed by axial canal.

Idiostroma, Winch. Coenosteum cylindrical or fasciculate, traversed by axial, tabulate zoöidal tubes, which give off secondary lateral tubes. General tissue reticulated, similar to *Stromatopora*. Devonian.

Stylodictyon, *Stromatoporella*, and *Syringostroma*, Nich.; *Amphipora*, Schulze; *Stachyodes*, Bargat. Devonian of Europe and North America.

A number of genera are described by Waagen and Wentzel from the Permo-Carboniferous rocks of Farther India, such as *Carterina*, *Disjectopora*, *Circopora*, etc.

Order 4. CAMPANULARIAE. Allman.

(*Leptomedusae*, *Calyptoblastea*, Allman; *Thecaphora*, Hincks.)

Delicate, branching, plant-like, sessile colonies, with chitinous periderm enveloping the base, pedunele, and also the cup-like receptacles (hydrotheeae) which enclose the

individual polyps. The proliferous zoöids are developed within urn-shaped capsules (gonothecae) of comparatively large size, and sometimes become separated off as free-swimming relate Medusae.

Although existing Campanularians (*Sertularidae*, *Plumularidae*, *Campanularidae*) are provided with a durable periderm, their remains have not as yet been detected in the fossil state, with the exception of a few forms from the Pleistocene. Nevertheless, in the Upper Cambrian, Ordovician, Silurian, and occasionally in the Devonian, numerous finely branching plant-like remains are found, which are sometimes furnished with a strong foot-stalk, and sometimes terminate acutely at the base; the original substance of which was undoubtedly chitinous. These forms are grouped together under the common term *Cladophora*, Hopkinson, and may be regarded as early types of the *Campanulariae*. Particularly well-preserved specimens exhibit on one or occasionally on both sides of the branchlets small cellules or hydrothecae, which evidently served for the reception of zoöids. Very often the branches are united by numerous slender transverse processes or dissepiments.

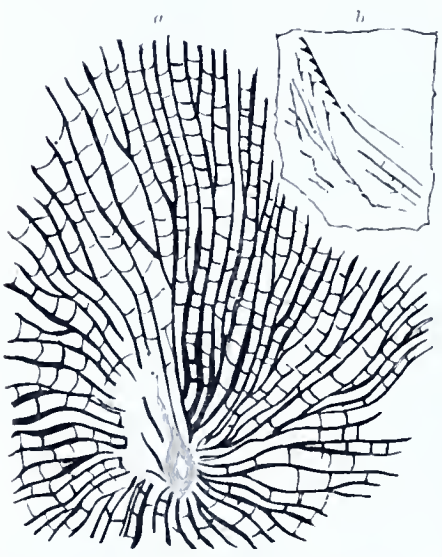


Fig. 201.

a, *Dictyonema retiformis*, Hall. Silurian (Niagara); Lockport, New York. Natural size. *b*, *Dictyonema*, sp. Branch-bearing hydrothecae. From Drift of Northern Germany (after Dames).

In the genera *Dendrograptus*, *Callograptus*, *Thamnograptus*, and *Inocaulis*, Hall; *Calyptograptus*, Spencer; *Bryograptus*, Lapworth, etc., the organisms are provided with a thick foot-stalk, by which they were probably attached to some foreign object. The branches are numerous, slender, often bifurcating, bear hydrothecae, and are connected by transverse processes.

Dictyonema, Hall (*Dictyograptus*, Hopkin.), (Fig. 201). Funnel- or fan-shaped branching fronds terminating acutely at the base, and probably unattached. Branches united at short intervals by dissepiments, and furnished distally on one side with hydrothecae; the latter, however, are rarely well preserved. Ordovician to Devonian. Particularly common in Ordovician rocks near Christiania, Norway, but usually compressed into fan-like networks.

Appendix to the Campanulariae.

Graptolitoidea, Lapworth (*Rhabdophora*, Allman).[1]

Under the term *Graptolitoidea* or Graptolites are included organisms which are generally found accompanying the *Cladophora* in Palaeozoic strata, and

[1] *Barrande, J.*, Graptolites de Bohême. Prague, 1850.—*Geinitz, H. B.*, Die Versteinerungen der Grauwackenformation in Sachsen. Leipsic, 1852. — Die Graptolithen des mineralogischen Museums in Dresden, 1890.—*Hall, J.*, Graptolites of the Quebec Group. Canadian Organic Remains, Decade II. (Geol. Surv. Canada), 1865.—*Herrmann, O.*, Die Graptolithen-Familie Dichograptidae, 1885.—*Holm, G.*, Gotlands Graptoliter (Bihang Svenska Vetensk. Ak. Handl. vol. XVI.), 1890.—On Didymograptus, Tetragraptus, etc. (Geol. Fören. Stockholm Förhandl. XVII.), 1895.—*Lapworth, C.*, Notes on the British Graptolites (Geol. Mag. vols. X. and XIII.), 1873-76. Also various papers

which have been considered by various authors as plant remains, horny sponges, *Pennatulidae*, Cephalopods, and Bryozoans. Portlock, in 1843, first pointed out their analogy with the Sertularians and Plumularians; and his inferences as to their common relationship were gradually corroborated by the painstaking researches of Allman, Hall, Hopkinson, Lapworth, Nicholson, and others. The Graptolites differ, however, from all existing *Hydromedusae*, and also from the closely related *Cladophora*, in the fact of their non-attachment, and in that a rod-like axis is almost invariably developed in the periderm.

Graptolites are generally found in an imperfect state of preservation, lying flattened in the same plane upon the slaty laminae in which they are embedded, and associated in large numbers. More rarely they occur in limestone, when the internal cavities are filled with calcareous matter, and the original form accurately preserved.

The general skeletal tissue (*periderm*) was obviously flexible, and composed of smooth or finely striated chitine; usually it has the form of a dense continuous membrane, but in the *Retiolitidae* it is attenuated and supported by a latticed network of chitinous threads. It is usually preserved as a thin bituminocarbonaceous film, which, however, is often infiltrated with pyrites, and is not infrequently replaced by a glistening greenish-white silicate (Gümbelite).

The organism or *hydrosoma* of the Graptolites is usually linear, more rarely petaloid in form, undivided or branching, and is either straight, bent, or in exceptional instances spirally enrolled. Cup-shaped hydrothecae, which are usually obliquely set and more or less overlapping, are borne on one or on both sides of the polypary, and are united by a common coenosarcal canal enclosed in the periderm. The polypary is strengthened by a peculiar chitinous axis (*virgula*, *solid axis*), which in the monoprionidian forms runs in a groove lying outside the coenosark on the dorsal side of the organism (*i.e.* on the side opposite to the polypiferous margin). But in the biserial Graptolites the virgula is generally double, and the two halves are either enclosed between the laminae of a central or sub-central septum, which is formed by the coalescence of the flattened dorsal walls (*Diprionidae*); or they are placed on opposite sides of the coenosark, and are united with the peridermal network (*Retiolitidae*). Very commonly the virgula projects at one or at both extremities, but notably at the distal end of the polypary, as a longer or shorter naked filament; its proximal extension is often called the *radicle*.

Springing from the common canal, which runs parallel with the virgula, is a series of hydrothecae (*thecae*, *cellules*, *denticles*), which are disposed in longitudinal rows along either one (Fig. 202), two (Fig. 203), or four sides of the polypary. They usually have the form of elongated, cylindrical, rectangular, or conical sacs; their walls are in most cases applied to those of their neighbours above and below, although occasionally they spring out quite isolated from one another. Each hydrotheca opens directly into the common canal, and is furnished distally with an external aperture, the form and size of which vary

in Quart. Journ. Geol. Soc., 1875, 1878, 1881, and in Annals and Mag. Nat. Hist. 1879, 1880.—*Nicholson, H. A.*, Monograph of the British Graptolitidae, 1872.—*Perner, J.*, Études sur les Graptolites de Bohême, 1894.—*Richter, R.*, Thüringische Graptolithen (Zeitschr. deutsch. geol. Gesellsch.), Bd. V., 1853; XVIII., 1866; and XXIII., 1871.—*Scharenberg, W.*, Ueber Graptolithen. Breslau, 1851. *Suess, E.*, Ueber böhmische Graptolithen (Haidinger's Naturw. Abhandl. Bd. IV. Abth. I.), 1851.—*Törnquist, S. L.*, Observations on Graptolites (Acta Univ. Lund. XXVI., XXVIII., XXIX.), 1890-92.—*Wiman, C.*, Ueber Monograptus und Diplograptidae (Bull. Geol. Inst. Upsala, I.), 1893. [Translated in Journ. Geol. vol. II. p. 267, 1893.]

extremely in different species. In some forms it is circular or quadrate, and upwardly directed; in others it is contracted and opens inferiorly, when the hydrothecae are bent downwards. Not infrequently the lower lip is ornamented with one or two slender spines, which often subdivide and inosculate with one another.

The polypary in most Graptolites is furnished at its proximal end with a minute, triangular, or dagger-shaped body called the *sicula* (Fig. 204), which represents the original embryonic skeleton. The first stage of development consists in the formation of an axis or virgula along the entire length of the sicula, which axis often projects freely at one or both extremities of the latter. Hydrothecae are then budded either uniserially along one side, originating from

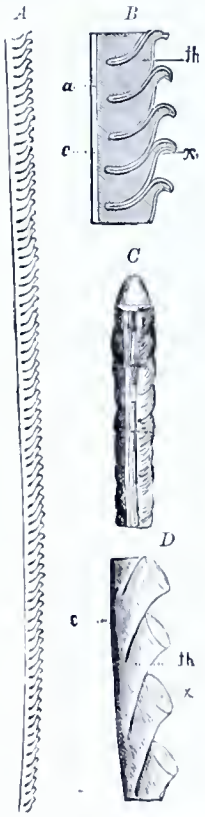


Fig. 202.

A, *C*, *Monograptus priodon*, Bronn. sp. Silurian (Etage E); Prague. *A*, Hydrosoma, natural size. *B*, Longitudinal section, enlarged. *C*, Dorsal aspect, enlarged. *D*, *Monograptus Bohemicus*, Barr. Same locality. *a*, Virgula; *c*, Common canal; *th*, Hydrothecae; *x*, External aperture (after Barrande).

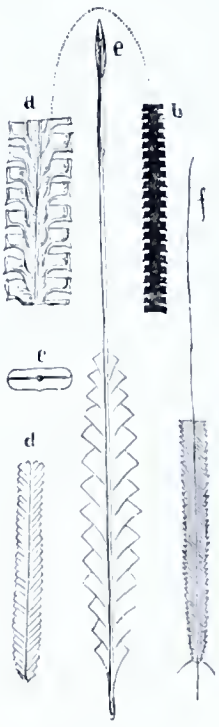


Fig. 203.

a, *c*, *Climacograptus typicalis*, Hall. Ordovician (Trenton limestone); Cincinnati, Ohio. *a*, Vertical section, enlarged, showing central virgula; *b*, Individual of the natural size; *c*, Cross-section, enlarged; *d*, *e*, *Diplograptus palmeus*, Barr. Silurian; Prague. Hydrosoma of the natural size and several times enlarged (after Barrande); *f*, *Diplograptus foliaceus*, Murch. Ordovician (Llandeilo Group); Scotland. Natural size (after Lapworth).

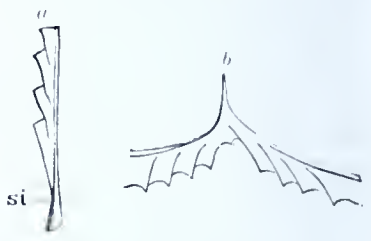


Fig. 204.

a, *Monograptus gregarius*, Lapw. Silurian; Dobbs Linn, Scotland. Proximal end showing sicula, enlarged; *b*, *Didymograptus pennatulus*, Hall. Ordovician (Quebec Group); Point Lévis, Canada. Proximal end showing sicula, enlarged (after Lapworth).

Fig. 205.

Diplograptus Whitfieldi, Hall. Silurian. Polypary furnished on both sides with gonangia, probably dehiscent. Natural size (after Hall).

near the major end of the sicula, or in alternate sequence along both of the lateral margins of the sicula; but in monoprionidian types the entire polypary is developed from the minor extremity of the sicula alone. The sicula itself ceases to grow, as a rule, after the first hydrothecae are budded, and sometimes it becomes obsolete or absorbed. In many cases it develops into a terminal

vesicle, or a filiform proximal virgula, or again into two spiniform or spur-like processes. Sometimes the hydrosoma remains undivided, sometimes it forms branches, which may diverge at various angles; in other cases two or four monoprionidian polyparies may be placed back to back with their dorsal walls coalescing, thus giving rise to di- or tetra-prionidian colonies. In the latter types the coenosark is commonly divided by one or two median septa, and the primordial buds originate at various distances along the sicular margin.

Occasional specimens of diprionidian Graptolites have been found bearing large sac-like or irregularly expanded corneous structures (Fig. 205), which are comparable with the ovarian capsules (*gonangia*) of recent Sertularians. Furthermore, the singular bodies known as *Dawsonia*—small, oval, bell-shaped, or conical chitinous capsules, which are often associated with Graptolites in vast numbers—are regarded by Nicholson as detached graptolitic gonangia.

Graptolites commonly occur in argillaceous schists, more rarely in limestone formations, of the Upper Cambrian, Ordovician, and Silurian systems. They seem to have swarmed in the muddier portions of the sea, and floated either as free-swimming colonies, or, in rarer instances, remained stationary with the sicula embedded in the mud. They are divided into three groups:—*Monoprionidae*, *Diprionidae*, and *Retiolitidae*.

Sub-Order A. MONOPRIONIDAE. Hopkinson.

Hydrothecae uniserially developed on the side of polypary lying opposite to the virgula.

Monograptus, Gein. (*Monoprion*, Barr.; *Pomatograptus* and *Pristiograptus*, Jaekel), (Figs. 202, 206). Hydrosoma undivided, rectilinear, or curved, sometimes helicoid. Hydrothecae in contact, usually overlapping. Aperture either entire or contracted, often directed downwards. Abundant from base to summit of Silurian.

Fig. 206.

a, *Monograptus Nilssoni*, Barr. Silurian (Alum Schists); Gräfenwerth, near Schleitz, Germany; *b*, *Monograptus colonus*, Barr. Silurian; Eliotsfield, Scotland. Showing sicula (after Lapworth); *c*, *Monograptus turriculatus*, Barr. Silurian; Prague (after Barrande). All figures natural size.

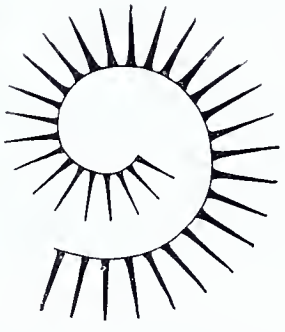


Fig. 207.

Rastrites Linnaei, Barr. Silurian; Zekkowitz, near Prague (after Barrande).

Fig. 209.

Didymograptus pennatulus, Hall. Ordovician; Point Lévis, Canada (after Hall).

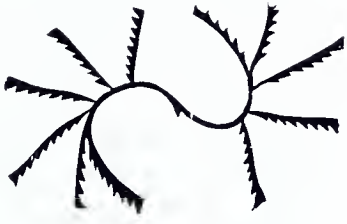


Fig. 208.

Coenograptus gracilis, Hall. Ordovician; Point Lévis, Canada (after Hall).

Fig. 210.

Tetragraptus bryonoides, Hall. Ordovician; Point Lévis, Canada (after Hall).

Rastrites, Barr. (Fig. 207). Hydrosoma simple, spirally coiled. Common canal very narrow, virgula attenuated; hydrothecae more or less linear, and separated from one another by considerable intervals. Silurian.

Leptograptus, Lapw. Hydrosoma consisting of two long, filiform, undivided, inequal primary branches, with hydrothecae developed from major extremity of the common sicula. Ordovician.

Coenograptus, Hall (Fig. 208). Two primary branches originating from the centre of a triangular sicula, curving sigmoidally, and giving off simple branches from the convex side at tolerably regular intervals. Ordovician.

Didymograptus, M'Coy (Figs. 209, 212, *a*). Two simple, symmetrically developed branches springing from a small axillary sicula. Hydrothecae having the form of flattened rectangular prisms, in contact throughout. Ordovician.

Tetragraptus, Salter (Fig. 210). Major extremity of sicula giving rise to a non-polypiferous connecting process (*funicle*) which sends off two simple branches at each end. Hydrosoma bilaterally symmetrical. Ordovician.

Dichograptus, Salter (Fig. 212, *b*). Hydrosoma consisting of eight simple

Fig. 211.

Dicranograptus ramosus, Hall. Ordovician (Hudson River); New York (after Hall).

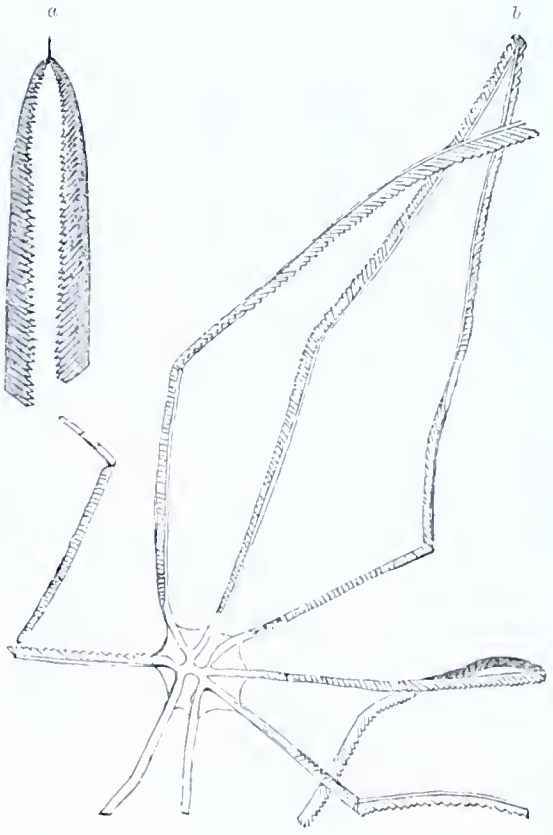


Fig. 212.

a, *Didymograptus Murchisoni*, Beck sp. Ordovician (Llandeilo Group); Wales. *b*, *Dichograptus octobrachiatus*, Hall. Ordovician (Quebec Group); Point Levis, Canada (after Hall).

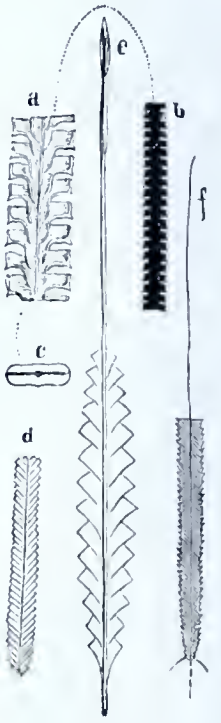


Fig. 213.

a, *c*, *Climacograptus typicalis*, Hall. Ordovician (Trenton limestone); Cincinnati, Ohio; *a*, Vertical section, showing common axis in the centre, enlarged; *b*, Polypary of the natural size; *c*, Cross-section, enlarged. *d*, *e*, *Diplograptus palmeus*, Barr. Silurian; Pragne; *d*, Polypary of the natural size; *e*, Polypary enlarged. *f*, *Diplograptus foliaceus*, Murch. Silurian (Llandeilo Group); Scotland. Natural size.

monoprionidian branches, which originate from as many subdivisions of the funicle; the latter often enveloped in a central corneous disk. Ordovician.

Dicranograptus, Hall (Fig. 211). Hydrosoma composed of two symmetrically developed branches which are coalescent in the proximal, and free in the distal portion of their length. Distal ends of hydrothecae isolated and incurved. Ordovician.

Sub-Order B. DIPRIONIDAE. Hopkinson.

Hydrosoma consisting of two or of four vertical rows of hydrothecae placed back to back, with the virgulae coalescing to form a central axis.

Diplograptus, M'Coy (Fig. 213, *d*, *f*). Hydrosoma linear, diprionidian. Hydrothecae rectangular in section, inclined, directly overlapping. Virgula embedded in a median septum, commonly projecting distally as a long fibre, and appearing proximally as a radicle. Primordial buds originating along whole length of sicular margins. Ordovician and Silurian.

Climacograptus, Hall (Fig. 213, *a*, *c*). Like the preceding, but with hydrothecae separated and standing nearly vertically; they are furthermore sub-oval in section, and distally somewhat contracted. Ordovician and Silurian.

Phyllograptus, Hall (Fig. 214). Hydrosoma leaf-like, and composed of four uniserial rows of prismatic hydrothecae coalescing along the whole length of their dorsal margins. Hydrothecae often with two lateral apertural spines. Base of the Ordovician.

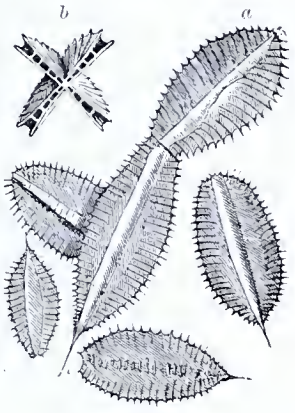


FIG. 214.

Phyllograptus typus, Hall. Ordovician (Quebec Group); Point Lévis, Canada. *a*, Several polyparies of the natural size; *b*, Ideal cross-section, enlarged (after Hall).

Sub-Order C. RETIOLITIDAE. Lapworth.

Coenosark of the common canal giving origin to a biserial polypary. Virgula either simple and central, or duplicate and attached to opposite sides of the periderm; the latter is much attenuated, and supported upon a network of chitinous fibres. Sicula absent.

Retiolites, Barr. (Fig. 215). Hydrosoma undivided, elongate, compressed, and tapering toward the extremities. Hydrothecae disposed in rows on each side of the axis, inclined, and in contact with one another. Virgulae two in number, separated, and attached to opposite sides of the peridermal network in the median plane of the hydrosoma; one is rectilinear, the other zigzag-shaped. Ordovician and Silurian.

Stomatograptus, Holm; *Retiograptus*, Hall; *Glossograptus*, Emmons. Ordovician.

Range and Distribution of the Hydrozoa.

Of the Hydrozoans in which preservation is at all possible, the *Hydrocorallinae* are known with certainty as far back as the Upper Cretaceous. During the Tertiary period they achieved a somewhat greater distribution, but have

only recently begun to enter extensively into the formation of coral-reefs and other calcareous deposits.

In the Upper Jurassic, notably in the Tithonian of the Mediterranean district, certain of the *Hydractinidae* (*Ellipsactinia*, *Sphaeractinia*) are very plentifully distributed; while, on the other hand, both the Triassic genus *Heterastridium*, and the genera *Parkeria* and *Porosphaera*, occurring in the Cretaceous of Northern Europe, belong to the rarer fossils.

Of vast importance as rock-builders, however, were the *Stromatoporoidea* of the Palaeozoic era. They occur profusely in the Ordovician and Silurian strata of North America, England, and Russia, and particularly in the Middle Devonian of the Eifel and Ardennes, as well as in Nassau, Devonshire, the Ural Mountains, Spain, etc. They frequently attain gigantic proportions, and are an essential constituent of the limestones and coral reefs of the Silurian and Devonian periods; but they do not survive beyond the Palaeozoic era.

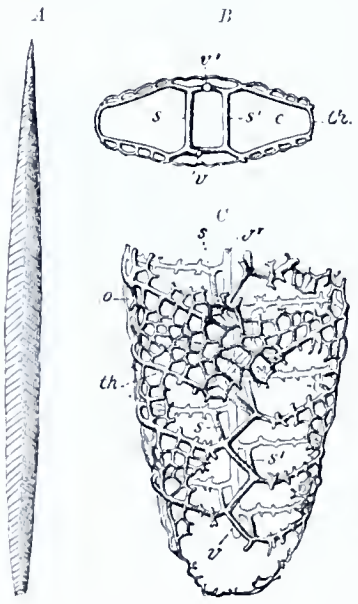


FIG. 215.

Retiolites Geinitzianus, Barr. Silurian. *A*, Specimen from silicious schists of Feuguerolles, Calvados; natural size. *B*, *C*, Polyparies from Motala, Sweden. *B*, Cross-section. *C*, Lower end, enlarged; calcareous matter dissolved out by acid. *v*, Zigzag-shaped virgula; *v'*, Rod-like virgula; *th*, Conjoined walls of hydrothecae; *s'*, Crossbars connecting the virgulae; *o*, Apertures (after Holm).

The *Graptolitoidea*, under which head the *Cladophora* are also commonly included, are confined to the Upper Cambrian, Ordovician, and Silurian periods. They are profusely distributed in the silicious schists and alum-slates of the Fichtelgebirge, Thuringia, Saxony, and Bohemia. They are plentiful also in the Harz, in Poland, Silesia, the Baltic Provinces, and the Ural district; and again in Scandinavia, Cumberland, Wales, the north of England, Scotland, and Ireland, as well as in Normandy, Brittany, Spain, Portugal, Sardinia, and Carinthia. In America they are found exquisitely preserved in Newfoundland, Canada, New York, Virginia, Tennessee, Ohio, Wisconsin, and Iowa. They are known also in South America (Bolivia) and Australia, and are not uncommon in the drift which covers the plains of Northern Germany.

According to Lapworth, the Graptolites are distributed vertically throughout six different horizons; the first of which coincides with the Upper Cambrian, the three following with the Ordovician, and the two uppermost with the Silurian. The *Monoprionidae* are especially characteristic of the two Silurian horizons.

Sub-Class 2. **ACALEPHAE.** Cuvier. Scyphomedusae.

(*Discophora*, Huxley.)

Free-swimming, discoidal, or bell-shaped Medusae, with downwardly directed mouth, with gastro-vascular pouches and numerous radial canals, and having, as a rule, the margin of umbrella lobed. Cambrian to Recent.

The Acalephs or Lobed Jelly-fishes, though frequently of considerable size, are entirely without hard parts, and therefore are singularly unfitted for preservation.

Under exceptionally favourable conditions, however, as in the Lithographic Slates (Upper Jurassic) of Eichstädt and Solenhofen, impressions of these delicate organisms are sometimes preserved, which admit of accurate systematic determination.

The best preserved and at the same time the most abundant species is *Rhizostomites admirandus*, Haeckel, belonging to the Acraspedote family of *Rhizostomidae*. Impressions also occur in flinty concretions of the Upper Cretaceous, which are most nearly referable to the Medusae. Of a more questionable nature are the organisms occurring in the Cambrian sandstone of Lugnaes, Sweden, and described by Torrell under the name of *Spatangopsis*, but which Nathorst assigns to the Acalephs. In the same strata also are found those peculiar fucoidal structures known as *Eophyton*, which are generally supposed to be of vegetable origin. Nathorst has brought forward evidence, however, to show that these may really have been produced by the trails of Jelly-fishes. Here also should be noticed the forms described by Nathorst as *Medusites*, from the Lower Cambrian of Sweden, which this author regards as casts of the gastric cavity of Jelly-fishes. According to Walcott, similar fossils are common in Alabama.[1]

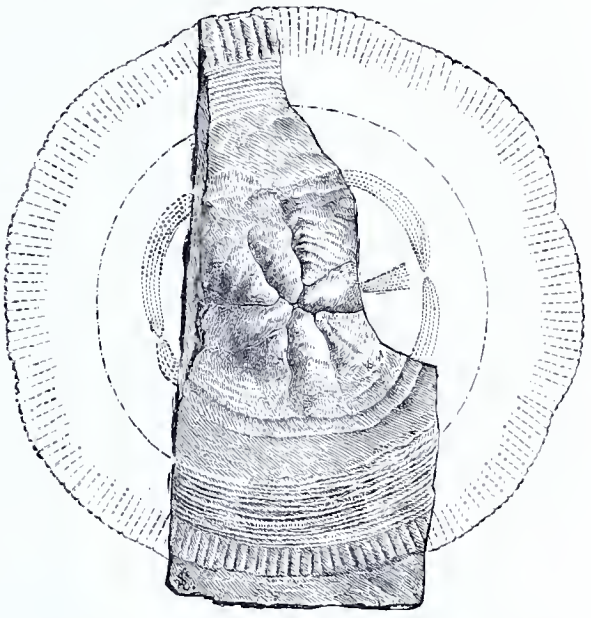


FIG. 216.

Rhizostomites admirandus, Haeck. Lithographic slates; Eichstädt, Bavaria. 1/7 natural size. (Missing parts restored in outline.)

[1] *Huxley, T.*, Memoir on the Anatomy and Affinities of the Medusae (Phil. Trans.), 1849.—*Kner, R.*, Ueber eine Meduse in Feuerstein (Sitzungsber. Wien. Akad. Bd. LII.), 1865.—*Haeckel, E.*, Ueber fossile Medusen (Zeitschr. für wissenschaft. Zool. Bd. XV. and XIX.), 1865 and 1870.—Neues Jahrb. für Mineralogie, 1866.—Jenaische Zeitschr. Bd. VIII., 1874.—System der Medusen, Bd. I. and II., Jena, 1880-81.—*Nathorst, A. G.*, Om Aftryck af Medusor, etc. (K. Svenska Vetensk. Akad. Handl., Bd. XIX.), 1881.—*Ammon, L. v.*, Ueber jurassische Medusen (Abhandl. k. baier. Akad. Bd. XVII.), 1883.—*Brandt, A.*, Ueber fossile Medusen (Mem. Acad. Imp. St. Petersb. vol. XVI., 7th Ser.), 1871. —*Pohlig, H.*, Altpermische Medusen (Festschrift zum 70ten Geburtstage R. Leuckarts), 1892.— *Hall, J.*, Palaeontology of N.Y., vol. I., 1847, and III., 1859.—20th Report N.Y. State Cabinet Nat. Hist., 1868.—*Lapworth, C.*, Notes on British Graptolites (Geol. Mag. X.), 1873.—*Hopkinson, J.*, and *Lapworth, C.*, Graptolites of the Arenig and Llandeilo rocks of St. David's (Quar. Journ. Geol. Soc. XXXI.), 1875.—*Linnarsson, G.*, and *Nicholson, H. A.*, On the vertical range of Graptolites in Sweden (Geol. Mag. III.), 1876.—*Lapworth, C.*, On Scottish Monograptidae (Geol. Mag. III.), 1876. —On the Graptolites of County Down (Ann. Rep. Belfast Nat. Field Club, I., Part IV.), 1877.— *Haupt, K.*, Die Fauna des Graptolithen-Gesteins (Neues Lausitzsches Mag. LIV.), 1878.—*Kayser, E.*, In Abhandl. geol. Specialkarte von Preussen II., Heft 4, 1878.—*Linnarsson, G.*, Om Gotland's Graptoliter (Svens. Vet.-Akad. Förh. XXXVI.), 1879.—*Lapworth, C.*, Distribution of the Rhabdophora (Ann. Mag. Nat. Hist. III.-VI.), 1879-80.—On new British Graptolites (*op. cit.* V.), 1880.— *Tullberg, S. A.*, On species of Didymograptus (Geol. För. Stockholm Förh. V.), 1880.—*Törnquist, S. L.*, Studier öfver Retiolites (Geol. För. Stockholm Förh. V.), 1881. Also papers by Törnquist and Linnarsson in same volume, pp. 292-326.—*Holm, G.*, Skandinavien's Graptoliter (Svens. Vet.-Akad. Förh. XXXVIII.), 1881.—*Tullberg, S. A.*, Skane's Graptoliter (Sven. Geol. Undersökn., Ser. C., I. and II.), 1882-83.—*Spencer, J. W.*, Graptolitidae of the Upper Silurian System (Bull. Univ. Mo. I., and Trans. St. Louis Acad. Sci. IV.), 1884.—*Jaekel, O.*, Ueber das Alter des Graptolithen-Gesteins (Zeitschr. deutsch. geol. Gesellsch. XLI.), 1890.—*Barrois, C.*, Mémoire sur la distribution des Graptolites en France (Annal. geol. soc. Nord), 1892.

Sub-Kingdom III. ECHINODERMATA

To the Echinoderms belong radially or bilaterally symmetrical animals, which were formerly included with the Coelenterates under the general category of *Radiata;* but were recognised by Leuckart as the representatives of a distinct animal type. They possess a well-developed, usually pentamerous dermal skeleton, which is composed of calcareous plates, or of minute, isolated, cal-

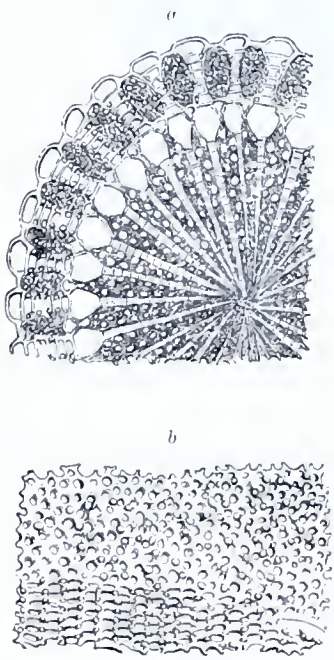


FIG. 217.

a, Magnified cross-section of an Echinoid spine; Fiji Islands. *b*, Magnified section of coronal plate of a recent Sea-urchin (*Sphaerechinus*); plane of section parallel to surface.

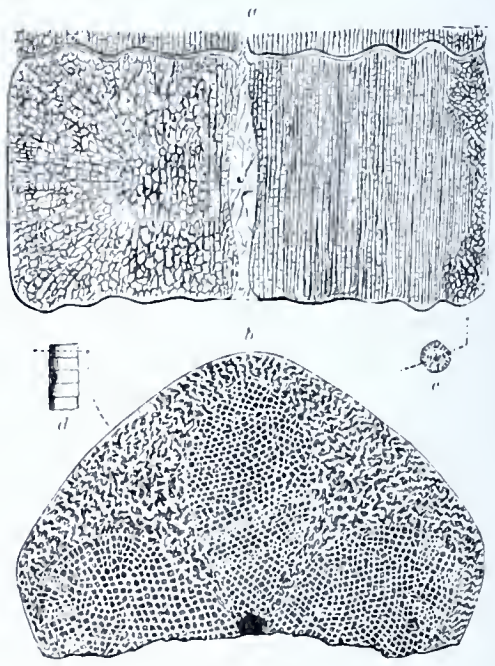


FIG. 218.

Pentacrinus subteres, Goldf. Upper Jura; Reichenbach, Wurtemberg. *a*, Vertical section of stem-joint in plane indicated in *c*. $^{18}/_{1}$; *b*, Transverse section of same. $^{18}/_{1}$; *c*, Joint-face; *d*, Side view of column (natural size).

careous bodies embedded in the integument; the exoskeleton may be more or less movable, or even immovable, but is very frequently provided with moveable appendages (spines, bristles, pedicellariae, etc.) The arrangement both of the skeletal parts and of the principal organs is so generally pentamerous, that five may be regarded as the fundamental numeral pervading the whole subkingdom of Echinoderms.

Apart from this constitutional difference, the Echinoderms are distinguished from the Coelenterates by the presence of a true digestive canal, a vascular system, and water-vascular apparatus; by a more perfectly developed nervous system; and by an exclusively sexual mode of reproduction.

The most striking difference consists clearly in the nature and composition of the exoskeleton (Figs. 217, 218). All of the plates, ossicles, spines, and other indurations are secreted in the integument (dermal connective tissue), and are all composed of microscopically small calcareous bodies embedded in organic matter. As these bodies are united to form perforated horizontal laminae, which are connected with one another by vertical pillars, the result is a minutely reticulated structure, highly characteristic of all Echinoderms. During fossilisation the interstices are commonly infiltrated with lime carbonate, so that the whole structure is transformed into calcite, exhibiting unmistakable rhombohedral cleavage. Each plate, joint, and spine of a sea-urchin, star-fish, or crinoid behaves mineralogically and optically like a single calcite crystal.

All the Echinoderms are marine. In the classification proposed by Haeckel they are divided into three primary groups comprising the following classes :—

Sub-branch A.	**Pelmatozoa.**	Class 1.	*Crinoidea.*	(Sea-lilies.)
		„ 2.	*Cystoidea.*	(Cystideans.)
		„ 3.	*Blastoidea.*	(Blastoids.)
Sub-branch B.	**Asterozoa.**	Class 1.	*Ophiuroidea*	(Brittle stars.)
		„ 2.	*Asteroidea.*	(Star-fishes.)
Sub-branch C.	**Echinozoa.**	Class 1.	*Echinoidea.*	(Sea-urchins.)
		„ 2.	*Holothurioidea.*	(Sea-cucumbers.)

Sub-Branch A. **Pelmatozoa.** Leuckart.

The *Pelmatozoa* are Echinoderms which, during the whole or at least the early portion of their existence, are fixed by a jointed, flexible stalk, or are attached by the dorsal or aboral surface of the body. The principal viscera are enclosed in a bursiform, cup-shaped, or spherical test (*calyx*), which is composed of a system of calcareous plates; and on the upper surface of which are situated both the mouth and anus, as well as the ambulacral or food grooves conducting to the mouth. As a rule, jointed flexible arms spring from the distal ends of the ambulacral grooves around the margin of the calyx; sometimes, however, arms are wanting, the ambulacral areas being extended down the sides of the calyx, and beset on both sides with pinnules (*Blastoidea*). The inferior (dorsal, aboral) portion of the calyx is composed of a single or double series of basal plates, which either rest directly upon the stalk, or are grouped about a centrodorsal plate.

The *Pelmatozoa* are divided into three classes :—*Crinoidea*, *Cystoidea*, and *Blastoidea*. Of these, only the Crinoids are represented by a few existing genera; the others are wholly extinct, and are confined, moreover, to the Palaeozoic rocks. Although the Cystideans possess a less highly specialised organisation than the others, and probably represent the common ancestral

type from which both the Blastoids and Crinoids have been derived, nevertheless, it is expedient to treat of the Crinoids first, since a knowledge of the anatomy in recent forms is essential to an adequate conception of the extinct.

Class 1. CRINOIDEA. Miller. Sea-lilies.[1]

(*Brachiata*, Bronn; *Actinoidea*, F. Roemer.)

Usually long-stalked, more rarely non-pedunculate and sessile, occasionally free-swimming Pelmatozoa with calyx composed of regularly arranged plates, and provided with well-developed movable arms.

The Crinoid organism consists of three principal elements—calyx, arms, and stalk. The calyx and arms together are sometimes spoken of as the crown, as contrasted with the peduncle.

1. *The Calyx.*—The calyx has usually the form of a cup-, bowl-shaped, or globular capsule, within which the more important organs are enclosed. Its lower (dorsal or abactinal) surface commonly rests upon a peduncle (Fig. 219); but in some forms it is attached directly by the base, and in rare instances it is free. The superior (ventral or actinal) surface is either membraneous or plated; it carries the mouth and ambulacral grooves, and hence is homologous with the under side of a star-fish or sea-urchin. As a rule, only the inferior and lateral portions (*dorsal cup*) of the calyx are visible, owing to the concealment of the summit by the arms. The cup is constituted of two or more circlets of plates, which are uniformly oriented with reference to the ambulacral organs.

a. By the *base* is understood the one or two rings of plates intervening between the topmost joint of the column and the first cycle of plates situated in the projection of the ambulacra or arms. When the basis is monocyclic (Fig. 220) the position of the proximal ring of plates is interradial; but when dicyclic it is radial, and the upper ring corresponds with the basals of monocyclic forms.

In the nomenclature of P. Herbert Carpenter, the upper series of plates in

[1] Literature:

Miller, J. S., A Natural History of the Crinoidea or lily-shaped Animals. 1821.
Müller, J., Ueber den Bau des *Pentacrinus caput medusae* (Abhandl. Berliner Akad.), 1841.
de Koninck, L. G., et *le Hon, H.*, Recherches sur les Crinoides du terrain carbonifère de la Belgique. Brussels, 1854. (Very extensive bibliography.)
Beyrich, E., Die Crinoideen des Muschelkalks (Abhandl. Berliner Akad.), 1857.
Schultze, L., Monographie der Echinodermen des Eifler Kalks (Denkschrift der k. k. Akad. der Wissenschaften), Vienna, 1866.
Shumard, B. F., Catalogue of Palaeozoic Echinodermata of North America (Trans. St. Louis Acad. Sci. vol. II.), 1868. (Very complete bibliography.)
Carpenter, W. B., On the Structure, Physiology, and Development of *Antedon rosaceus* (Philosophical Transactions Royal Society, vol. CLVI.). 1876.
Wachsmuth, C., and *Springer, F.*, Revision of the Palaeocrinoidea. I.—III. (Proc. Acad. Nat. Sci. Philad.), 1879-86.
Wachsmuth, C., and *Springer, F.*, Discovery of the Ventral Structure of *Taxocrinus* and *Haplocrinus*, *ibid.*, 1888.
Wachsmuth, C., and *Springer, F.*, The Perisomic Plates of Crinoids. *ibid.*, 1890.
Wachsmuth, C., and *Springer, F.*, The Crinoidea Camerata of North America. (In preparation.)
Loriol, P. de, Paléontologie Française. Crinoides Jurassiques, I.—II., 1882-89.
Neumayr, M., Die Stämme des Thierreichs. Band I., 1889.
Agassiz, A., *Calamocrinus Diomedae* (Memoirs Museum Comp. Zool. vol. XVII.), 1892.
Bather, F. A., British Fossil Crinoids (Ann. and Mag. Nat. Hist. (6th ser.), vols. V.—VII.), 1890-92.
Bather, F. A., The Crinoidea of Gotland (K. Svenska Vetensk. Akad. Handlingar, vol. XXV.), 1892.

the dicyclic forms are properly termed *basals*, and the lower series *underbasals* (*infrabasals*). The basals as thus defined are equivalent to the "parabasals" in

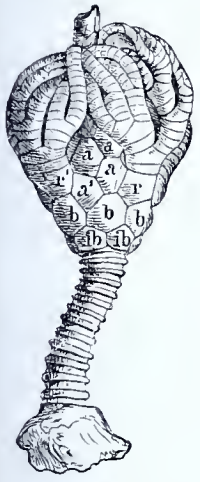


FIG. 219.

Euspirocrinus spiralis, Ang. Stalked Crinoid with dicyclic base and anal interradius. *a*, Anals; *b*, Basals; *ib*, Infrabasals. (Right and left sides reversed, after Angelin.)

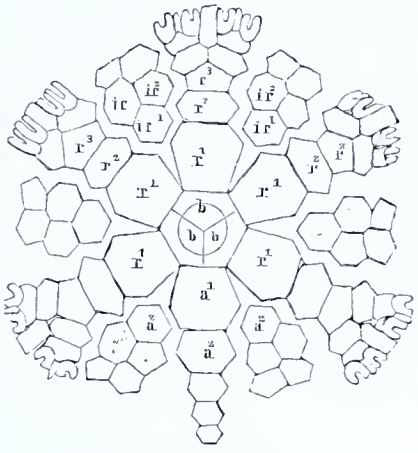


FIG. 220.

Actinocrinus proboscidialis, Hall. Projection of calyx showing the three basals (*b*), 5×3 simple radials (*r*), four paired interrays (*ir*), and a fifth unpaired anal interray (*a*).

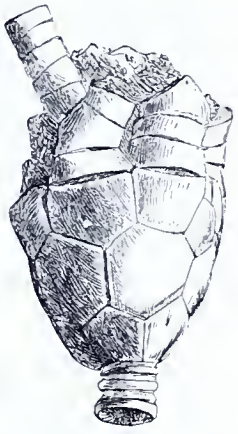


FIG. 221.

Poteriocrinus multiplex, Traut. Calyx with dicyclic base, radials, costals, and distichals.

the older nomenclature of Johannes Müller, and to the "subradials" of de Koninck and other authors.

Both basals and infrabasals are primarily five in number; but owing to the fusion of two or more of the proximal plates, the number of basals in the monocyclic forms may be reduced to four, three, or even to two, and that of infrabasals in the dicyclic to three. During the ontogenetic development of the recent *Antedon*, a more or less complete resorption of the basals has been observed; and the same probably also held true for certain Mesozoic genera (*Eugeniacrinus*, *Phyllocrinus*). In many of the non-pedunculate Crinoids (*Uintacrinus*, *Marsupites*, Fig. 222) an additional plate known as the *centrodorsal* rests against the infrabasals, and probably represents an atrophied stalk. The basals are united with one another and with the overlying radials by close sutures, and are immovably held together by fibrous connective tissue. Though usually smooth, the joint faces are sometimes striated, and are visible externally as incised lines.

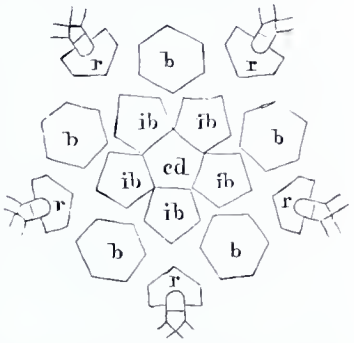


FIG. 222.

Marsupites testudinaris, Schlot. sp. Diagram of calyx. *cd*, Centrodorsal; *ib*, Infrabasals; *b*, Basals; *r*, Radials.

b. Succeeding the base is a cycle of five (rarely four or six) plates, which, on account of their position with reference to the rays, are called *radials*. The radials form the sides of the calyx in nearly all Mesozoic and Recent Crinoids, and give origin directly to the arms, which may become free immediately above the radials, or may be incorporated for some distance in the calyx, either by means of supplementary plates, or by lateral suture among themselves.

The upper boundary of the calyx is differently demarcated by different authors. Many assign all the plates above the first cycle of plates in each ray to the arms, even when they are immovably united with one another at the sides; while, according to Schultze and others, the arms begin invariably at the point where they first become movable, *i.e.* above the first articular facet. The latter course is open to serious objections, inasmuch as strictly homologous parts receive different appellations in different groups.

Carpenter, Wachsmuth, and Bather restrict the term "radial" to the lowermost circlet of radially situated plates, and speak of the succeeding cycles as far as and including the first axillary plate as *brachials* (distinguished as first, second, and third costals, distichals, and palmars respectively), in all cases, whether the plates are free or fixed.

In most Palaeozoic Crinoids one or more *interradial plates* are intercalated between two of the rays, and in line with the anal aperture; these are called the anal plates or *anals*. If a plane be passed through the latter and through the radial situated directly opposite, the calyx will be divided into two symmetrical halves: the parts lying to the right or left when viewed from the

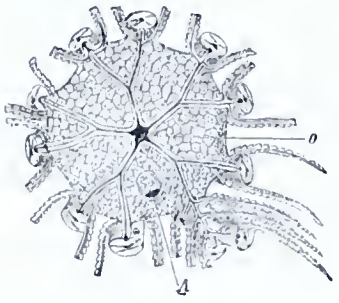


Fig. 223.

Pentacrinus caput-medusae, Lam. sp. Ventral disk constructed of very thin perisomic plates, with central mouth (*o*), open ambulacra, and eccentric anus (*d*).

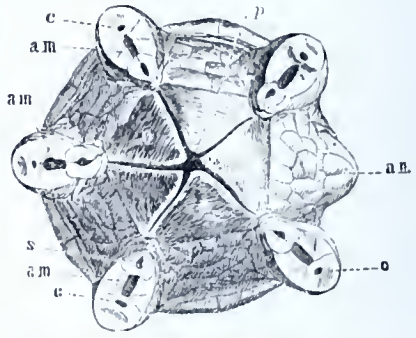


Fig. 224.

Hyocrinus Bethellianus, Wyv. Thom. Recent. Ventral disk, enlarged. *o*, Orals; *p*, Mouth (*peristome*); *s*, Covering plates; *c*, Dorsal canals of the arms; *am*, Ambulacral furrows of the arms; *an*, Anus (after Wyville Thomson).

posterior or anal side are so designated; while the anterior side is that opposite the anal interray. Interradial plates, however, are not confined to the anal interray, but are frequently developed also between the other rays, when the calyx is correspondingly expanded. If several cycles of radials are present, an equal number of interradials are also developed, and are distinguished in like manner as interradials and distichal interradials of various orders. The anal interray is frequently characterised by the peculiar number, size, and position of the anal plates.

c. The superior side of the calyx is known as the *tegmen calycis*. The covering may be in the form of a coriaceous skin, in which large numbers of thin calcareous ossicles are embedded (Figs. 223, 224), or of a plated disk rising from the base of the arms. It frequently exhibits a more or less central, externally visible mouth-opening, and a usually eccentric interradial anal aperture. The mouth opens into an oesophagus and thence into the expanded visceral mass, which fills the greater portion of the inner cavity. The intestinal canal is directed downwards at first, and after numerous windings discharges into the anal opening. In certain fossil Crinoids (*Actinocrinidae*) the digestive

apparatus is represented by an extremely thin-walled, finely perforated, convoluted body, which occupied the vertical axis of the body cavity, and was contracted into a narrow tube toward the base (Fig. 232).

In all recent Crinoids five (occasionally four) open ambulacral furrows lined with epithelium conduct from the mouth to the tips of the arms, remaining either simple or subdividing as often as there are arms. Underneath the floor of the grooves runs an ambulacral vessel filled with water; and accompanying this are the blood and vascular canals and a nervous cord. Distensible tentacles pass out from alternate sides of the ambulacra, and the latter unite to form a circumoral *ring canal*. From the ring canal five short open tubes (*stone* or *water canals*) extend downwards into the body cavity and supply the ambulacral system with water.

In the recent genera, *Thaumatocrinus*, *Rhizocrinus*, *Calamocrinus*, *Hyocrinus* (Fig. 224), and in a large number of fossil Crinoids, a triangular *oral plate* is situated in each of the five angles of the mouth-opening. The apices of the

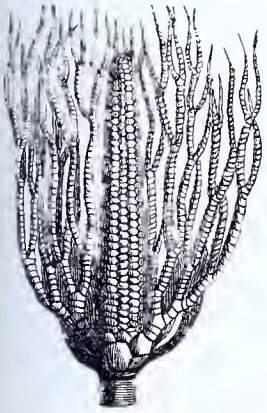


Fig. 225.

Lecythocrinus Eifelianus, Müller. Crinoid with elongated anal tube (after Schultze)

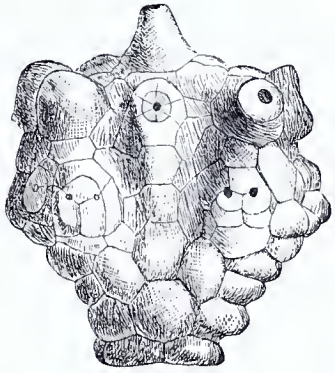


Fig. 226.

Dorycrinus quinquelobus, Hall sp. Specimen showing plates of the tegmen and eccentric anus.

Fig. 227.

Coccocrinus rosaceus, Roem. Devonian; Eifel. Calyx with ventral pavement, twice enlarged (after Schultze).

orals are directed towards one another, and between them run the ambulacra. The plates are extremely variable in size; and although well-developed in the larvae of *Antedon* and *Pentacrinus*, they become wholly resorbed before maturity. In a number of Palaeozoic Crinoids (*Larviformia*, Fig. 227) the summit is entirely or in large part composed of five oral plates which may be either laterally in contact or separated by furrows. More frequently, however, the orals occupy only the angles of the mouth-opening, the remaining area between the ambulacral furrows being covered with more or less regularly arranged *interambulacral plates* (Fig. 224). In most of the Palaeozoic *Camerata*, and the recent *Calamocrinus*, the anus is placed at the upper end of a tube known as the *anal tube* or *proboscis*. In the *Fistulata*, however, the anal opening is situated along the anterior side of the ventral sac, or between the sac and the mouth.

Of the interambulacral plates a greater or smaller number (in *Calamocrinus* all in the vicinity of the mouth) are perforated by respiratory pores for the admission of water into the inner cavity. Pores evidently performing a similar office occur in some of the *Fistulata;* but these, instead of piercing the

body of the plates, enter only their outer angles. Other *Fistulata* have a madreporite.

The ambulacra are frequently lined along their sides by perpendicular, wedge-shaped *side-plates*, and these are surrounded by movable *covering pieces*, both of which extend from the mouth to the ends of the arms. In the Palaeozoic *Taxocrinus* (Fig. 228), the covering pieces are arranged in alternate rows, with side pieces adjoining them. The latter plates occur also in most of the *Fistulata* and *Articulata*, but are rarely represented in the *Camerata*. The mouth may be exposed or closed; being either surrounded by five oral plates (*Taxocrinus*, Fig. 228), or the posterior oral may be pushed in between the four others, so as to conceal the mouth; the latter is then said to be *subtegminal* (Fig. 229).

A very remarkable modification of the ventral disk occurs in the Palaeozoic *Camerata*. Here the usually very numerous plates attain considerable thickness, and fit into one another like the stones of an arch to form an extremely rigid, more or less convex vault, which is sometimes surmounted by an equally rigid plated proboscis. At the apex of the dome five large-sized plates are often

Fig. 228.

Taxocrinus intermedius, W. and S. Ventral disk (after Wachsmuth and Springer.)

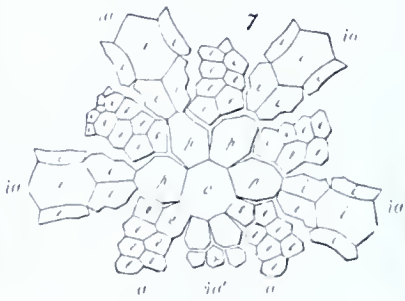


Fig. 229.

Platycrinus Halli, Shum. Projection of ventral disk. *a*, Ambulacrals; *ia*, Interambulacral areas; *ia'*, Anal interradius; *c*, Covering pieces of the ambulacrals; *i*, Interradials; *p*, Anterior and lateral orals; *o*, Posterior (anally situated) oral; *x*, Plates of the anal interambulacral area (after W. and S.)

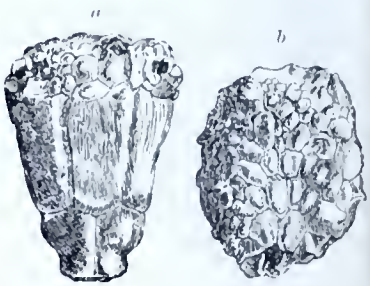


Fig. 230.

Hexacrinus elongatus, Goldf. Calyx with tegmen. *a*, Profile; *b*, Aspect from above.

distinguishable, of which that lying in the anal interradius commonly differs from the rest in form and size, and appears to be wedged in amongst the others. These five plates are identified by Wachsmuth and Springer as orals. The remainder of the tegminal plates are distinguished according to their position as ambulacrals and interambulacrals; in most of the *Actinocrinidae* the ambulacrals are not arranged in alternate rows (Fig. 231), but frequently consist of large single plates of one or more orders, which are separated from one another by the continuous interposition of supplementary pieces. In other groups, notably the *Platycrinidae*, the ambulacra are generally arranged in two rows of rather large plates, which, however, lose their original character to some extent. The interambulacrals usually meet with the interbrachials. The tegmen of the *Camerata*, as a rule, is composed of large nodose plates, for the identification of which considerable experience is required.

Most of the Palaeozoic Crinoids have but a single opening in the tegmen, which is interradial in position, and undoubtedly represents the anus. With the exception of the *Ichthyocrinidae* the mouth is subtegminal, and the food grooves are rigidly closed. In many cases the covering pieces are pushed

inward, and the ambulacra follow the inner floor of the tegmen, forming a skeleton of ramifying tubes; these are conducted along open galleries from the mouth to the arm-openings (Fig. 232, *A*).

2. *The Arms* (*Brachia*).—The arms of the Crinoid body form the immediate prolongation of the radials. The plates of the arms are termed *brachials*, and

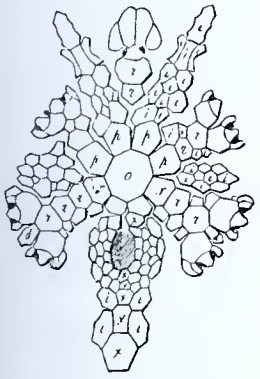


Fig. 231.

Agaricocrinus Americanus, Roem. Ventral disk. *r*, Uniserial ambulacrals; *i*, Interambulacrals; *o*, Anally situated oral; *p*, Anterior and lateral orals; *x*, Posterior interambulacrals (after Wachsmuth and Springer).

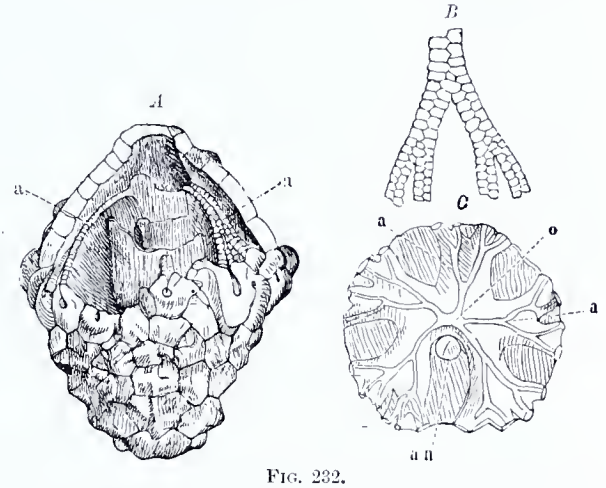


Fig. 232.

Actinocrinus proboscidialis, Hall. *A*, Plates of tegmen partially removed in order to show the covered ambulacral passages (*a*) leading from the arms to the mouth. *B*, Plated upper surface of ambulacral galleries. *C*, Natural cast of ventral disk with impressions of calyx ambulacra (*a*) leading to the mouth (*o*); *an*, Anus.

are arranged either in single or double alternating rows; and hence are spoken of as uniserial (Fig. 233, *A*), or as biserial (Fig. 233, *B*). The plates of the uniserial arms may be either rectangular or cuneiform, the major ends being directed alternately to the right and left. In biserial arms the smaller ends of

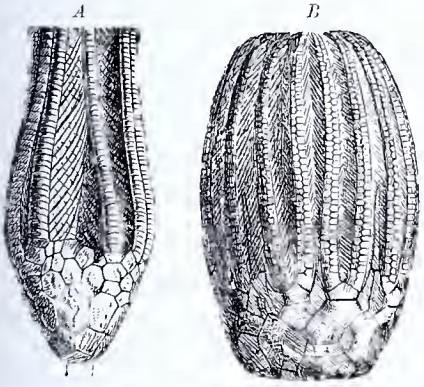


Fig. 233.

A, *Carpocrinus comtus*, Ang. sp., showing uniserial arms. *B*, *Callicrinus costatus*, Hising., with biserial arms (after Angelin).

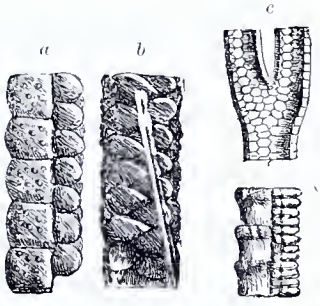


Fig. 234.

Plated ambulacral furrows of the arms. *a*, *b*, *Cyathocrinus ramosus*, Ang., showing covering pieces; *c*, *Gissocrinus arthriticus*, Hising., with covering pieces. All figures enlarged.

the plates meet midway, so as to form a zigzag suture. The arms invariably begin uniserially, the biserial structure being gradually introduced in an upward direction. The arms either remain simple, or branch in various ways; the plates upon which a bifurcation takes place are called *axillaries*.

In the *Camerata*, the more highly organised *Fistulata*, and in all recent

Crinoids, the arms are furnished with *pinnules*, which are given off alternately from opposite sides, one to each arm-plate. The pinnules are jointed appendages, which repeat the general structure of the arms, and in living Crinoids lodge the genital organs. When two or more arm-joints meet transversely by a rigid suture, and only the upper one is pinnule-bearing, those joints form a *syzygy*, whether their apposed faces are striated, dotted, or smooth. The lower joint bearing no pinnule is called the *hypozygal* joint, the upper one the *epizygal*: and the two together constitute physiologically but a single segment, as is shown by the alternation of the pinnules.

Both arms and pinnules are traversed ventrally by a deep groove (*ambulacral* or *arm furrow*), at the bottom of which is situated a tubular prolongation of the body cavity (the so-called *coeliac* or *dorsal canal*); overlying the latter run the genital, water, and vascular canals, a nervous cord, and two rows of tentacles. The furrows of the arms enter by the *arm-openings* into the tegmen, and all converge to the mouth. Food-particles, consisting chiefly of diatoms, infusorians, and microscopic crustaceans, are propelled along the furrows and into the body by the action of cilia.

In all recent and in numerous fossil Crinoids the arms are perforated in the dorsal half by a single, or in some cases by a duplicate axial canal (*axial cord*), containing elastic fibres and a nerve-band, the latter frequently giving off delicate branches with ramifications in every direction. The dorsal canal extends also into the radials and basals, perforating the plates when they are thick, and running in a shallow groove on the inside when thin. So far as has been observed, the axial canals begin uniformly in the basals, where they divide dichotomously; but in the radials the branches generally reunite to form the so-called *ring canal* (Fig. 276).

3. *The Column.*—The stem or column attains in some forms (*Pentacrinus*) a length of a number of metres; but in others it is much abbreviated, or even atrophied, so that the calyx is either directly adherent by the base (*Cyathidium*), or is destitute of all means of attachment (*Astylocrinus*, *Uintacrinus*, *Marsupites*, *Antedon*). The stem is composed of short segments, having either circular, elliptical, or angular (especially pentagonal) cross-sections, and being sometimes of uniform and sometimes of variable proportions. Lateral appendages, called *cirri*, are present in numerous forms, being given off either singly or in whorls at certain intervals along the periphery. The larger and all cirrus-bearing segments are called *nodal joints*, and those interposed between them the *internodal joints*. The distal end of the stalk may taper gradually to an apex, in whose vicinity fine radicular cirri are commonly developed, or, it may be thickened at the extremity so as to form a bulbous or branching root. Growth is accomplished by the insertion of new joints at the proximal end of the stem, the earlier segments becoming at the same time gradually enlarged. The last formed joints are commonly of smaller size than those situated more remotely from the calyx. In the early stages of *Antedon* the column is terminated distally by a large so-called *dorsocentral* plate.

All the joints of both the stem and cirri are pierced by a central longitudinal canal, which is either round or pentagonal in cross-section, and communicates with a peculiar dorsally situated *chambered organ*. The latter is supposed to represent the central nervous system, but contains in addition a vascular organ that has been regarded as a kind of heart. The axial canal of the stem is encased in a sheath of elastic tissue which serves to bind the in-

dividual segments together. The union is further strengthened by sutures, the apposed faces of the joints being for the most part flat, and either radially striated, or diversified in various ways by prominences and grooves, the grooves being likewise occupied by connective tissue. Sometimes the apposed faces are smooth and rigidly united with one another (*Encrinus*, etc.); but in other cases an articulation is secured by means of an elevated usually oblique fulcral ridge (*Rhizocrinus*, *Bourgueticrinus*). The proximal segments of the column occasionally exhibit simple vertical clefts which indicate an original quinquipartite composition. These divisions always occur alternately with those of the basals in monocyclic, and with those of the infrabasals in dicyclic forms.

Ontogeny. — Although we are acquainted as yet with the life-history of but the single genus *Antedon*, the phenomena of its development are of such significance as to shed most valuable light upon many conditions observed in fossil Crinoids. Following impregnation, the ova perform the early stages of development within the ovarian glands of the pinnules. Immediately after escaping from the vitelline membrane the embryo is girded with four transverse ciliated bands, possesses a laterally situated mouth, and bears considerable resemblance to certain Annelid embryoes. Delicate plates of calcareous network (which, when definitely developed, are ten in number) are next formed within the wider anterior portion of the gastrula larva; these are arranged in two transverse rings, the plates of the anterior series being placed symmetrically above those of the posterior. Extending from the centre of the lower row downwards and backwards, a series of delicate calcareous rings may now be observed, at the base of which a large cribriform plate is rapidly developed. The two rows of plates gradually become enlarged, and the outline of the rudimentary calyx is more clearly defined, while sheaves of parallel calcareous rods are seen passing through the rings of the rudimentary stalk. The hitherto free-swimming larva now becomes fixed, the ciliated bands disappear, the outer surface becomes invested with a thick sarcode layer, and the mouth appears as a large patent opening occupying the centre of the cup. The five plates surrounding the mouth are termed the orals, and the five constituting the proximal series the basals, which rest directly upon the topmost segment (centrodorsal) of the stalk. In the five diamond-shaped spaces which are left between the divisions of the orals and basals delicate net-like plates (radials) are next formed, which increase rapidly in size and intrude upon the orals. At the same time a sixth plate (anal) makes its appearance in the zone of radials, but is gradually forced upward with the orals into the ventral disk. Rows of elongate cylindrical segments (brachials), which grow very rapidly, are next given off by the radials, when the larva is said to have reached the "Pentacrinus stage." Simultaneously with the development of the arms and column, a resorption of the anal and orals occurs, which plates are obliterated on the completion of the dermal skeleton. The basals also become obsolete, owing to the encroachment of the centrodorsal, and are indicated in the adult form by a mere rudiment in

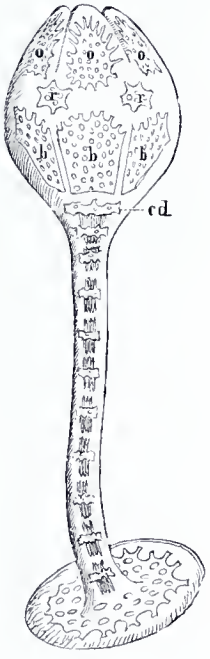


FIG. 235.

Larva of *Antedon rosaceus*, Linck. *b*, Basals; *r*, Radials; *o*, Orals; *cd*, Centrodorsal (after Wyville Thomson).

the form of a small ring-like rosette. Finally, the button-shaped centrodorsal, which is now beset with numerous cirri, detaches itself from the stalk, and the creature becomes capable of independent motion.

The ontogeny of *Antedon* reveals the fact that the basals, orals, and stem represent the most primitive skeletal structures, while the radials and brachials are formed at a subsequent period. Similar evidence is afforded by numerous fossil Crinoids, in which the basals and column are very strongly developed, while the radials are mostly of inferior size, and the arms either rudimentary or absent.[1]

Habitat.—Existing Crinoids live together in large numbers, and inhabit depths ranging from shallow water to a maximum of about 3000 fathoms. Their distribution, however, is mostly very local. Fossil Crinoids also appear to have been gregarious in habit, and their remains are frequently found commingled with those of reef-building corals in Palaeozoic strata. Owing to the extremely delicate constitution of many of the skeletal parts, and the looseness with which the plates and segments are united, the Crinoid organism is by no means favourably adapted for preservation in the fossil state. Perfect crowns are of comparatively rare occurrence; but, on the other hand, detached joints of the stem and arms are often very abundant, and occasionally form beds of considerable thickness. Crinoidal limestones of greater or lesser extent are met with in numerous formations from the Ordovician to the Jura; those of the Carboniferous and Muschelkalk (Trochitenkalk) being especially characteristic.

Classification.—The first attempt to construct a classification of the Crinoids was that of J. S. Miller in 1821. Four groups differing in the form and mode of union of the calyx plates were distinguished by Miller, as follows:—*C. articulata*, *semiarticulata*, *inarticulata*, and *coadunata*. The classification of Johannes Müller, in 1841, was based upon a number of differential characters, such as the articular or close suture of the radials, the thickness of the calyx plates, the mobility of the arms, and the plated or coriaceous character of the ventral disk. Two principal groups were recognised: *Articulata* and *Tesselata*; while a third (*Costata*) was constructed for the reception of the unique genus *Saccocoma*. T. and T. Austin and F. Roemer adopted the untenable divisions of Stalked and Unstalked Crinoids.

The importance of Wachsmuth and Springer's investigations on the structure of the calyx, especially of the tegmen, and on the orientation of the stem and its canals in monocyclic and dicyclic forms, cannot be overestimated. Two groups were put forward in their classification of 1879: *Palaeocrinoidea* and *Stomatocrinoidea* (= *Neocrinoidea*, Carpenter); groups which correspond in the main with the *Tesselata* and *Articulata* of Johannes Müller. This classification was subsequently abandoned, and a new one proposed for it in 1888, in which four principal orders were recognised, as follows: *Camerata*, *Inadunata*, *Articulata*, and *Canaliculata*; the latter being nearly identical with the *Articulata* of Müller. The *Inadunata* are further divided into the two suborders—*I. larviformia* and *I. fistulata*; but it is preferable to regard these groups

[1] [Some of the *Ichthyocrinidae* are almost identical, in fact, with the pedunculate stages of *Antedon*. Wachsmuth and Springer, from their observations on the orientation of the stem and its canal in fossil monocyclic and dicyclic Crinoids, were led to infer the presence of infrabasals in the nepionic or adult stages of many forms previously supposed to be without them. This prediction was abundantly confirmed by Mr. Bury's discovery of minute infrabasals in the gastrula larva of *Antedon*. See especially *H. Bury*, Early Stages in the Development of Antedon rosaceus, Philos. Trans. vol. CLXXIX. pp. 257-301, 1889.—TRANS.]

as of equal value with the remaining orders. The divisions established by Wachsmuth and Springer are on the whole extremely well founded, and have been adopted as the basis of the following systematic arrangement. The term *Inadunata* is dropped, however, on raising the *Larviformia* and *Fistulata* to the rank of independent orders; and for the terms *Articulata* and *Canaliculata*, the designations *Flexibilia* and *Articulata* are substituted respectively.

[More recently an improved classification has been prepared by Wachsmuth and Springer, in connection with their as yet unpublished monograph on the Crinoidea Camerata of North America. The primary divisions of the *Crinoidea* as now recognised by these authors are shown in the subjoined table.

Within the last few years, also, the terminology has been amended in several important respects; and conformably to the usage of the leading English and American authorities, certain of these changes have been adopted in the present edition. An explanatory note on the use of terms is therefore given at this place, in order to facilitate reference, and to exhibit the correspondence between the older terminology and the new.

The only abbreviations employed in the text are the following:—

IB = Infrabasals. *Br* = Brachials.
B = Basals. *RA* = Radianal.
R = Radials. *IRA* = First or special anal.

In addition to these the following are used in the figures, but are printed in small letters:—

K = Calyx. *O* = Orals.
A = Arms. *IR* = Interradials.
St = Stem. *Dist* = Distichals.

Explanation of Terms.

Crown = Crinoid minus the stem.
Calyx = Crinoid skeleton minus the stem and free arms.
Dorsal cup = All parts of the calyx below the origin of the free arms.
Tegmen = That part of the calyx lying above the origin of the free arms, and embracing the disk ambulacra, the mouth, and the anus. Includes the terms *ventral disk*, *vault*, *dome*, *summit*, etc.
Base = That part of the dorsal cup lying next to the column. It may be composed of one or of two rings of plates, which are distinguished as *basals* and *infrabasals*. The basals adjoin the radials and alternate with them, being interradial in position. The infrabasals, when present, form the proximal ring, and are radially disposed.
Radials = The circlet formed by the first plate in each of the rays; or, the radially situated circlet of plates above basals, and this ring only. In some of the earlier Crinoids one or more of the radials are transversely bisected, in which case the two parts are distinguished as *superradial* and *inferradial*. (Abbreviated R^1 in the figures.)
Brachials = All plates beyond the radials in radial succession. They are called *fixed* brachials so far as they take part in the calyx; *free* brachials or *arm-plates* when they do not. The brachials forming the first circlet above the radials, whether free or fixed, are called *primary* brachials, or *costals*; those of the second order *distichals*, or secondary brachials; those of the third order *palmars*; and all succeeding brachials, whether there are additional divisions in the ray or not, receive the name *post-palmars*.
Interradials = All plates occupying the spaces between the rays proper, whether they belong to the dorsal cup or the ventral disk. Those of the dorsal cup, which are interposed between the brachials, are distinguished as *interbrachials*, and those of the tegmen, which lie between the ambulacra, as *interambulacrals*.
Anals = Interradials of the posterior side, forming the base of the anal structure. The *special* or *first anal* plate, when present, invariably rests upon the truncated upper face of the posterior basal, and between the radials. Higher anal plates may be present, even when the special anal is wanting; they are interposed between the interbrachials following the median line of the posterior area.

The *Radianal* (=*first* or *lower anal plate* auct.), when present, rests within the re-entrant angle of two adjoining basals to the right of the true anal plate, and is the lower half of a bisected radial, which only in certain genera assumes anal functions.

Orals=The five large interradial plates which surround the mouth or cover it. They are said to be *symmetrical* when of nearly the same size and form; *asymmetrical* when the posterior plate is pushed in between the four others.

Ambulacrals=The rows of small plates in the tegmen which are radially situated. They consist of *adambulacrals* or *side-pieces*, and the *covering-plates* (*Saumplättchen*). The former, when present, constitute the outer, the latter the inner rows of plates. The covering plates form a roof over the food-grooves; they are generally represented by two alternating rows of small plates, more or less regular in their arrangement, which are movable upon the arms and pinnules, but upon the disk only in those Crinoids in which the mouth is exposed.

The *orientation* is based upon the natural position of the Crinoid, with the arms uppermost, and viewing the specimen from the anal side. The anal interradius will then be posterior, the radius opposite to it anterior, while the right and left sides correspond with right and left of the observer.

Primary Divisions of the Crinoidea, according to W. and Sp.

I.

Crinoids in which the arms are free above the radials. The topmost joint the youngest in the stem.—Order 1. INADUNATA.

(*a*) Disk composed of orals only. Ambulacra subtegminal.—Sub-Order A. *Larviformia.*
(*b*) Posterior side of the disk extended into a sac. Ambulacra suprategminal.—Sub-Order B. *Fistulata.*

II.

Crinoids in which the lower brachials take part in the dorsal cup. All plates of the calyx united by close sutures. Mouth and food-grooves closed. The top joint the youngest in the stem.—Order 2. CAMERATA.

III.

Crinoids in which the lower brachials are incorporated into the calyx either by lateral union with each other, or by means of a skin studded with calcareous particles. All plates from the radials up movable. Mouth and food-grooves exposed. The top stem joint fused with the infrabasals, and not the youngest joint of the stem.—Order 3. ARTICULATA.

(*a*) Arms non-pinnulate.—Sub-Order A. *Impinnata.*
(*b*) Arms pinnulate.—Sub-Order B. *Pinnata.*]

Order 1. LARVIFORMIA. Wachsmuth and Springer.

(*Haplocrinacea*, Neumayr.)

Tegmen formed by five triangular orals only, arranged in the form of a pyramid. Dorsal cup composed of basals and radials exclusively, except in the Cupressocrinidae, where the basals enclose a central undivided plate. All plates immovably united by close sutures; arms feebly developed. Ordovician to Carboniferous.

Mostly small forms exhibiting embryonic characters persistently throughout life.

Family 1. Haplocrinidae. Roemer.

Calyx small, pyriform to globose. Three of the radials compound, the others simple. Orals large, triangular to pentagonal, laterally in contact. Arms five, uniserial, non-pinnulate. Devonian.

Haplocrinus, Steining. (Fig. 236). *B* five, *R* five, unequal. Three of the radials composed of two pieces, of which the uppermost or *superradial* is the larger, and bears an articular facet for the attachment of the arms. Arms small, simple, uniserial, resting within deep grooves formed along the sides of the orals. Orals large, pentagonal, and laterally in contact; the posterior one pierced by a small anal opening. Mouth subtegminal; column composed of thin joints. Not uncommon in the Middle Devonian of the Eifel and Nassau; sparse in the Upper Devonian of North America.

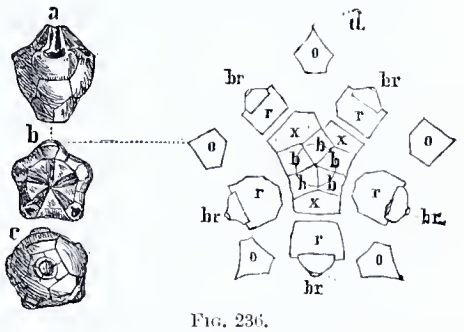


Fig. 236.

Haplocrinus mespiliformis, Goldf. Devonian; Gerolstein, Eifel. *a*, Calyx seen from one side; *b*, Seen from above; *c*, Seen from below; *d*, Diagram of calyx; *b*, Basals; *x*, the three unsymmetrical plates situated between basals and radials; *r*, Radials; *br*, First arm-ossicle; *o*, Orals.

Family 2. **Allagecrinidae.** Etheridge and Carpenter.

Calyx very small. Basals five, radials five, of irregular form and size. Some of the radials axillary and supporting two arms; others truncate and supporting but one arm; their articular facets provided with transverse ridges and large muscle plates. Upper Sub-Carboniferous; Europe and North America.

Allagecrinus, E. and C. *B* completely anchylosed in the adult, and the suture lines between the orals also disappearing with age. Stem largest next to the calyx, rapidly tapering downward. Sub-Carboniferous; Great Britain and North America.

Family 3. **Pisocrinidae.** Angelin.

Calyx small, globose or cup-shaped, and composed of heavy plates. Basals three to five, radials five, very unequal, the right posterior one compound. Inferradial completely roofed over by the lateral flanges of the superradial and right antero-lateral radial. Arms simple, uniserial, and composed of long, cylindrical joints. Silurian and Devonian.

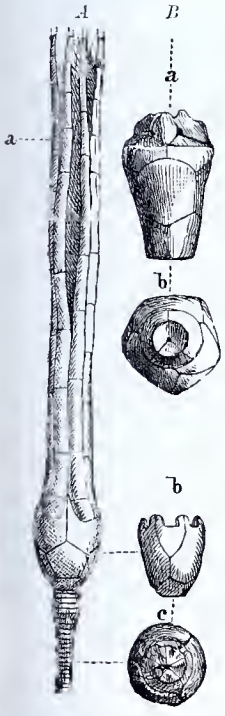


Fig. 237.

A, *Pisocrinus flagellifer*, Ang. Silurian; Gottland. *a*, Perfect specimen, posterior view; *b*, Calyx seen from one side; *c*, From below. 1/1 (after Angelin). *B*, *Triacrinus altus*, Müll. Devonian; Gerolstein, Eifel. *a*, Calyx seen from one side; *b*, From below. 1/1.

Pisocrinus, de Kon. (Fig. 237, *A*). *B* five, unequal, forming a triangle. Only the large anterior radial, and the left posterior resting upon the basals; the superradial of the right posterior ray, and the right antero-lateral radial, being supported by the upper angle of the inferradial; the latter not in contact with the anal tube. Articular facets of the radials impressed between vertical partitions formed by the lateral margins of the plates. Tegmen rarely preserved; but, as observed by Wachsmuth in *P. pilula*, consisting of five large symmetrical orals, above which rises a long, narrow, anal tube. Arms long, and composed of extremely elongate, heavy, cylindrical ossicles. Silurian; Gottland, Dudley, England, and North America (Niagara Group).

Triacrinus, Münst. (Fig. 237, *B*). Differs from the preceding in having but three *B*. Wachsmuth has shown, however, that some of the Eifel specimens occasionally have five *B*, thus leading to the inference that the two forms are identical. Devonian; Eifel, Fichtelgebirge.

Family 4. **Symbathocrinidae**. Wachsmuth and Springer.

Calyx small, bowl-shaped, composed of three unequal or of five equal basals, and five nearly equal radials. Tegmen formed by five small, asymmetrical orals; between these and the radials extends a long, anal tube, which, however, is not supported by anal plates. Entire upper edges of the radials bevelled off so as to form straight articular facets, which are furnished with well-developed transverse ridges. Arms five, simple; column round. Devonian and Carboniferous.

Symbathocrinus, Phill. *B* three, unequal; *R* five, long, quadrangular or pentagonal. The posterior oral larger than the others. Anal tube long, very slender, resting partly upon the radials and partly upon the orals. Arms long, uniserial, and composed of comparatively thick ossicles with sharp angular edges. Carboniferous; Great Britain and North America.

Phimocrinus, Schultze. Differs from the preceding in having five *B*. Devonian; Europe.

Stylocrinus, Sandb. Distinguished from *Symbathocrinus* mainly by the character of the radial facets, which are directed obliquely downward and inward, instead of upward and outward. Devonian.

Stortingocrinus, Schultze. Devonian. *Lageniocrinus*, de Kon. Carboniferous.

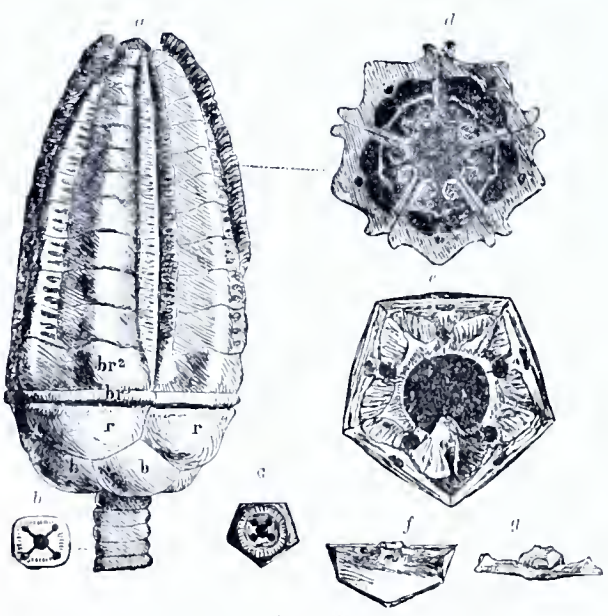


Fig. 238.

Cupressocrinus crassus, Goldf. Devonian; Gerolstein, Eifel. *a*, Perfect specimen, natural size; *b*, Cross-section of column; *c*, Centrodorsal plate; *d*, Section through the folded-up arms, showing well-preserved inrolled pinnules, plated covering of ambulacral furrows, and neuro-vascular canals perforating the ossicles; *e*, Interior of calyx from above, showing the five consolidating plates; the lowermost containing the anal opening; *f*, Radial pierced by ambulacral opening, but with wall covering, the same partly broken away; *g*, Side-view of radial in which the ring-like covering of the ambulacral opening is preserved intact.

Family 5. **Cupressocrinidae**. d'Orbigny.

Calyx large, basin-shaped, composed of five equal basals and five equal radials; the basals enclosing a central pentagonal plate, which in all probability represents five anchylosed infrabasals. Upper faces of radials broad, truncate, and forming an even horizontal line. Costals compressed, flange-shaped. A peculiar annular structure, the so-called "consolidating apparatus," situated on the upper interior margin of the calyx between the arm-bases. Arms five, simple, uniserial, and closely folded; they are composed of broad thick plates united by close sutures, and are traversed by a well-developed dorsal canal. Column pierced by a large axial and three, four, or five peripheral canals. Devonian.

Cupressocrinus, Goldf. (Fig. 238). Tegmen very small; the greater part of the ventral surface covered by the so-called consolidating apparatus. This is composed of five petaloid, horizontally truncated interradial pieces, which are laterally in contact, and enclose a large, central open space. The opening was probably covered by orals, as in *Symbathocrinus;* while the consolidating plates served for the attachment of muscles. Five round apertures, through which the ambulacra entered the calyx, perforate the divisions between the consolidating plates; one of the latter is pierced by the anal opening (Fig. 238, *e*). Arms provided with a wide and deep ventral furrow, lined on both sides with jointed, closely abutting appendages; of these there are several to each arm-plate, thus showing that they are different from true pinnules. Middle Devonian; Eifel, Harz, Nassau, and Westphalia. *C. crassus, elongatus, abbreviatus*, Goldf.

Myrtillocrinus, Sandb. Calyx deep; tegmen formed by five large symmetrical orals resting directly upon the radials. *IB* fused into a single plate, and pierced by the quadripartite canal of the stem. Devonian.

Family 6. **Stephanocrinidae.** Wachsmuth and Springer.

Calyx cup-shaped, composed of three elongate basals, five radials, and five interradials. Radials deeply forked; the prongs formed by the margins of two contiguous radials extending upward between the arms, and building together with the interradials a row of pyramids. Radial incisions occupied by the ambulacral grooves, which are roofed over by two rows of covering pieces; those of the same row closely anchylosed. First costals semilunate, and resting within a horseshoe-like concavity near the outer end of radial incisions. Tegmen constituted of five large triangular orals. Arms very short, composed of about ten pieces, all of which are axillary, and give off side arms. The latter are biserial, non-pinnulate, and are made up of long, strongly cuneiform joints. Ordovician and Silurian.

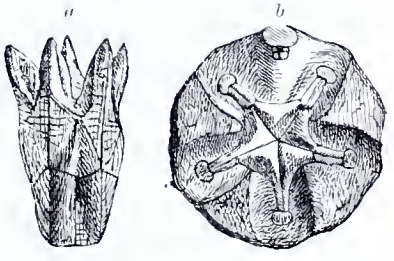


Fig. 239.

Stephanocrinus angulatus, Conrad. Silurian; Lockport, New York. *a*, Side view of calyx, natural size; *b*, Summit aspect, enlarged; projecting upper ends of the radials broken away (after Hall).

Stephanocrinus, Conrad (*Rhombifera*, Barr.), (Fig. 239). This unique genus is distinguished from all other *Larviformia* by the biserial and branching character of the arms, as well as by the presence of small interradials. Anal aperture situated near the summit of one of the interradial projections. Ordovician (Etage D); Bohemia. Silurian; North America.

Order 2. CAMERATA. Wachsmuth and Springer.

(*Sphaeroidocrinacea*, Neumayr.)

The lower arm-plates incorporated into the dorsal cup by means of supplementary plates. All plates of the calyx united by close sutures, and immovable. Tegmen in the form of a solid vault, composed of rigidly united plates. Mouth- and food-grooves completely covered; the covering pieces of the latter frequently incorporated in the tegmen. Anal opening eccentric or subcentral, frequently situated at the end of a proboscis-like anal tube. Interradials constantly present in all interrays; inter-

distichals and interpalmars often, and in most cases anals also present. Arms uniserial or biserial, and pinnulate. Ordovician to Carboniferous.

[**Analysis of Families, according to Wachsmuth and Springer.**[1]

I.

Lower brachials and interbrachials forming an important part of the dorsal cup.

A.—Interradials Ill-Defined.

The lower plates of the rays more or less completely separated from those of other rays, and from the primary interradials, by irregular supplementary pieces. Anal interradius divided by a row of conspicuous plates. Dicyclic or monocyclic.—Reteocrinidae.

B.—Interradials Well-Defined.

1. *Dicyclic*—

(*a*) Radials in contact except at the posterior side.—Thysanocrinidae.
(*b*) *Radials separated all around.*—Rhodocrinidae.

2. *Monocyclic*—

(*a*) *Radials in contact all around.*

Symmetry of the dorsal cup, if not strictly pentamerous, disturbed by the introduction of anals between the brachials only.—Melocrinidae.
Arms borne in compartments formed by partitions attached to the tegmen. Dorsal cup perfectly pentamerous. Calyx plates limited to a definite number.—Calyptocrinidae.

(*b*) *Radials in contact except at the posterior side, where they are separated by an anal plate.*

First anal plate heptagonal, followed by a second between two interbrachials.—Batocrinidae.
First anal plate hexagonal, followed by two interbrachials without a second anal. Arms branching from two main trunks by alternate bifurcation.—Actinocrinidae.

II.

Brachials and interbrachials but slightly represented in the dorsal cup.

1. *Dicyclic*—

Radials in contact except at the posterior side.—Crotalocrinidae.

2. *Monocyclic*—

(*a*) *Radials in contact all around. Base pentagonal.*—Platycrinidae.
(*b*) *Radials separated at the posterior side by an anal plate. Base hexagonal.*

Basals followed directly by the radials.—Hexacrinidae.
Basals separated from radials by accessory pieces.—Acrocrinidae.]

Family 1. **Platycrinidae.** Roemer.

Dorsal cup composed of a monocyclic base and a circlet of five large radials, without special anal plate. The lower brachials, which form part of the calyx, similar in form and size to the free arm-joints. Interradials heavy, restricted almost exclusively to the tegmen; only those of the first row to a certain extent interbrachial. Arms often numerous, generally free from the distichals upwards; uniserial or biserial. Pinnules well developed. Silurian to Carboniferous.

[1] [*Wachsmuth, C.*, and *Springer, F.* The Crinoidea Camerata of North America (Memoirs Museum Comp. Zool. vol. xxiv.) In press. The above is extracted from proof-sheets kindly furnished by the authors.—Trans.]

Platycrinus, Miller (Figs. 229, 240). *B* three, unsymmetrical, frequently anchylosed. *R* long, large, laterally united by close sutures, and furnished superiorly with a crescent-shaped articular facet. Succeeding the *R*, and united with them by close sutures, is a row of small axillaries. These are often so minute as to be completely hidden within the radial facets, as is also the case sometimes with the first distichals. First row of interradials on a level with the arm-bases, and consisting of three plates horizontally arranged; they are in part interbrachial and in part interambulacral. The higher interradials, when present, strictly interambulacral; plates of the anal interray more numerous than those of the four regular sides. Orals large, asymmetrical, and resting against the interradials. Covering pieces of the ambulacra generally exposed, very rigid, and incorporated into the tegmen. Anus either eccentric, or placed at the end of a short thick tube. Arms uniserial at their lower ends, but gradually becoming biserial. Column elliptical and twisted; the axes of the upper and lower surfaces of the individual segments being slightly shifted upon one another. The stem is pierced by a very minute axial canal, and gives off cirri toward the distal end. Extremely scarce in Devonian, but abundant in Carboniferous. *P. laevis*, Mill.; *P. hemisphaericus*, M. and W.

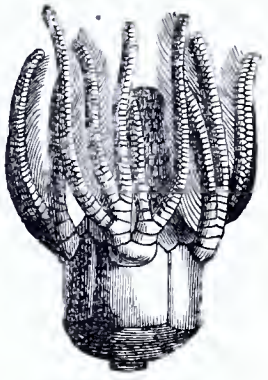


Fig. 240.

Platycrinus trigintidactylus, Austin sp. Carboniferous Limestone; Tournay, Belgium (restored after de Koninck).

Eucladocrinus, Meek. Calyx and stem as in *Platycrinus*, but having the rays produced laterally into large tubular appendages, from which biserial, pinnule-bearing arms are given off alternately throughout their entire length. Sub-Carboniferous (Burlington and Keokuk Groups).

Coccocrinus, Müller (Fig. 227). Like *Platycrinus*, but the costals wider, and forming together with the interradials a part of the dorsal cup. Costals two, succeeded by two distichals, of which the upper one is axillary; interradials only one to each side. Orals large, triangular, abutting against the interradials, and forming nearly the whole of the ventral surface. They are separated from one another by a deep angular groove, closed at the bottom. Anal opening in the suture between the posterior interradial and its corresponding oral. Silurian; Tennessee. Devonian; Eifel.

Culicocrinus, Müller. Transitional between *Coccocrinus* and *Platycrinus*. Calyx, as in the former, small and globose; but the orals somewhat asymmetrical. Arms bifurcated, heavy, biserial. Column round. Middle Devonian; Eifel.

Cordylocrinus, Ang. Arrangement of calyx plates as in *Platycrinus*, but the tegmen higher, and arms uniserial. Column round, and bearing long cirri; the upper ones reaching nearly to the tips of the arms. Silurian; Gottland.

Marsupiocrinus, Phill. Dorsal cup depressed, saucer-shaped. *B* and *R* as in *Platycrinus*. Radials rapidly spreading, and followed by a very small trigonal axillary; this, together with the two superjacent distichals, is buried within the radial facet, so that the three plates are wholly or almost wholly supported by the radials. Tegmen composed of numerous small pieces; anal opening eccentric. Column round, and traversed by a large axial canal. Silurian; Gottland, England, and North America (Niagara Group).

Family 2. **Hexacrinidae.** Wachsmuth and Springer.

Dorsal cup composed of a monocyclic base, five large radials, and an anal plate similar in form and size to the radials interposed between them. In all other respects constituted like the Platycrinidae. Devonian and Carboniferous.

Hexacrinus, Austin (Fig. 241). *B* three, equal; *R* five, very large and elongate. Tegmen low, composed of relatively large plates, and pierced by an eccentric anal opening. Arms uniserial or biserial; pinnules unusually long. Column round. Devonian; represented by numerous species in England, France, Belgium, and the Eifel, but by only a few in North America.

Dichocrinus, Münst. Differs from *Hexacrinus* in having but two hexagonal basals, and an eccentric anal opening. Sub-Carboniferous; Belgium. Great Britain, and North America.

Arthrocantha, Williams (*Histricrinus*, Hinde). Like *Hexacrinus*, except that the calyx plates are beset with short mobile spines. Devonian; North America.

Pterotocrinus, Lyon and Cass. *B* two, equal. *R* short, rapidly spreading: their upper faces excavated for the reception of several orders of brachials,

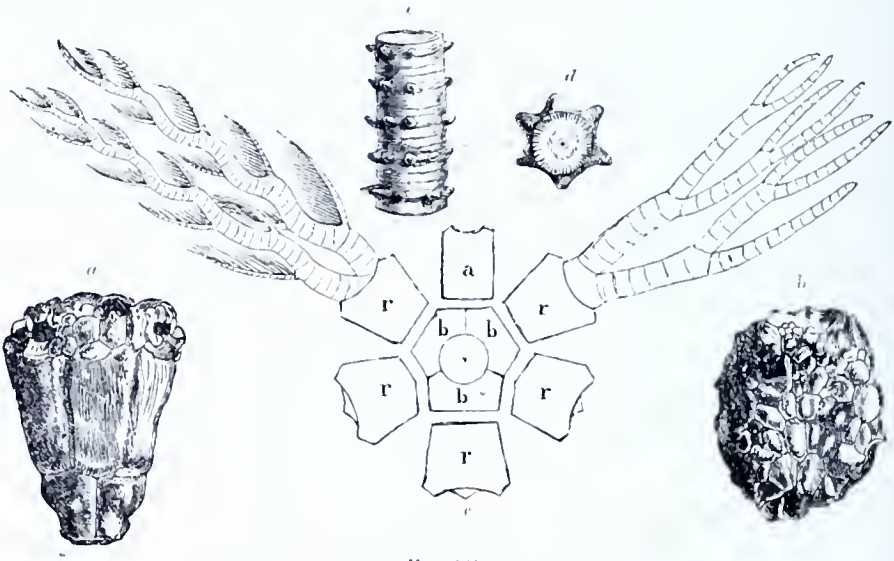


Fig. 241.

Hexacrinus elongatus, Goldf. Devonian; Pelm, Eifel. *a*, Calyx seen from one side; *b*, Aspect of summit; *c*, Diagram of calyx and arms; *d*, *e*, Column of *H. spinosus*, Mull. (after L. Schultze).

which rest with their lateral edges upon it; all of these plates taking part in the dorsal cup. *IRA* less than half the size of the *R*, and sometimes triangular. Tegmen highly elevated, pyramidal. Orals large, asymmetrical; their lower angles enclosing five large, radially disposed plates, which are separated from one another by interambulacral pieces. These plates are provided with enormous, leaf-like, club-shaped, or spatulate processes, which project outward conspicuously from between the arms. Anus sub-central. Arms four to each ray; biserial. Kaskaskia Group; North America.

Talarocrinus, W. and Sp. Intermediate between the preceding and *Dichocrinus*; structure of the tegmen resembling the former, that of the dorsal cup the latter. *IRA* slightly smaller than the *R*; its upper end narrower than

the lower. Costals one to each ray, very minute, trigonal; they are roofed over by the distichals, which rest with their sides upon the *R*, but are laterally in contact with one another. Processes of the tegmen thorn-like and less prominent than in *Pterotocrinus*. Arms two to four. Anus sub-central. Confined to the St. Louis Limestone of North America.

Family 3. **Actinocrinidae**. Roemer.

Base monocyclic. Basals three, sub-equal; radials united laterally, except at the posterior side, where they are separated by a large anal plate. Fixed brachials large, similar in form to the radials. Interradials abundantly represented; the first row interposed between the primary brachials, and consisting of a single plate in each of the interrays except the posterior; the second row consisting of two or three plates, and usually succeeded by additional rows. Plates of the tegmen numerous, and forming a rigid vault. Orals markedly asymmetrical; anus sub-central, eccentric, or marginal, with or without an anal tube. Ordovician to Middle Sub-Carboniferous.

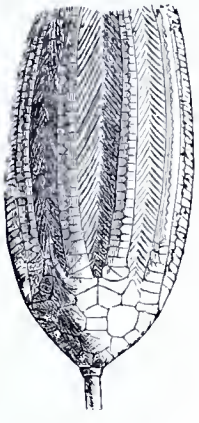


Fig. 242.

Patelliocrinus leptodactylus, Ang. sp. Silurian; Gottland. Natural size (after Angelin).

[The *Actinocrinidae*, Roemer, according to Wachsmuth and Springer, fall naturally into two subdivisions, which are elevated by them in their forthcoming Monograph to the rank of independent families. The relations between the two sections, which are designated as groups *A* and *B* in the original, and the genera embraced by them, are as follows:—

A. (Actinocrinidae, s. str.), *IRA* hexagonal, succeeded by two interbrachials without a second anal. (*Actinocrinus*, *Cactocrinus*, *Amphoracrinus*, *Teleiocrinus*, *Steganocrinus*, *Physetocrinus*, *Strotocrinus*.)

B. (Batocrinidae, W. and Sp.), *IRA* heptagonal, succeeded by two interbrachials which enclose a secondary anal. (*Batocrinus*, *Eretmocrinus*, *Dorycrinus*, *Agaricocrinus*, *Alloprosalocrinus*, *Barrandeocrinus*, *Habrocrinus*, *Desmidocrinus*, *Periechocrinus*, *Megistocrinus*, *Abacocrinus*, etc.]

(Section A.) Actinocrinidae.

Actinocrinus, Miller (Fig. 243). Calyx pyriform or ovate; plates of the dorsal cup generally ornamented with striae passing from plate to plate. *B* three, equal, forming a hexagon. Three of the *R* six-sided, generally higher than wide; the posterior pair heptagonal. First costals nearly as high as wide; second costals axillary, supporting both distichals and palmars, and frequently higher orders of brachials. *IR* very numerous, passing insensibly into the tegmen; anus sub-central, and borne at the end of a large, strong anal tube. Arms biserial; not bifurcating in their free state, or rarely so; and given off in clusters from lateral expansions of the calyx. Pinnules long, slender, and laterally in contact. Column long, round; its joints frequently sharply edged, and with striated upper and lower faces. Abundant in Sub-Carboniferous of North America and Europe.

Cactocrinus, W. and Sp. Like the preceding, except that the arms form a continuous ring around the calyx, and the *IR* of the dorsal cup are separated from those of the tegmen. Sub-Carboniferous; North America.

Amphoracrinus, Austin. Dorsal cup, saucer-shaped or almost flat; tegmen

highly elevated. Arms heavy; branching in the free state. Anus borne at the end of a short, stout, spinous tube. Lower Sub-Carboniferous; North America and Europe.

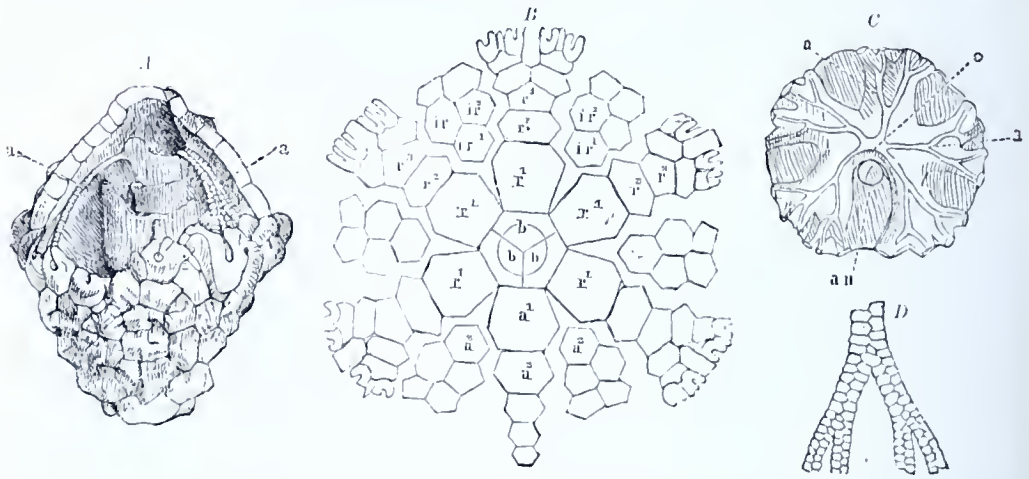


Fig. 243.

A, *Actinocrinus proboscidialis*, Hall. Sub-Carboniferous; Burlington, Iowa. Calyx with fractured tegmen, showing the subtegminal ambulacral skeleton, and the convoluted digestive organ. *B*, Diagram of *Dorycrinus*. *C*, Natural cast of tegmen of *Physetocrinus*, with impressions of food-grooves (*a*), conducting from the arms to the mouth (*o*); *an*, Anus. *D*, Enlarged portion of the ambulacral skeleton (after Meek and Worthen).

Teleiocrinus, W. and Sp. Arms closely crowded, and forming a broad continuous flanging rim around the calyx. Anus at the upper end of a long tube. Upper Burlington Limestone.

Steganocrinus, Meek and Worth. Burlington Limestone.

Physetocrinus, M. and W. Arms crowded; the arm-bases projecting in a rim, which is interrupted along the interrays. Anus in the form of a circular opening through the tegmen. Lower Sub-Carboniferous; North America, England, and Belgium.

Strotocrinus, M. and W. Arms crowded; the upper part of the dorsal cup produced in an immense rim, which is horizontally directed, and is composed of higher orders of brachials. Tegmen flat; composed of innumerable minute pieces. Anus in the form of an opening through the tegmen. Restricted to the Upper Burlington Limestone.

Fig. 244.

Batocrinus pyriformis, Shumard sp. Sub-Carboniferous; Burlington, Iowa. Nat. size (after Meek and Worthen).

(Section B.) Batocrinidae.

Batocrinus, Cassed. (Fig. 244). Similar in form to *Actinocrinus*, but calyx plates without sculpturing. *R* hexagonal or heptagonal. First costals quadrangular, always shorter than the *R*, and transversely arranged. *IRA* of the same size as the *R*. Interradials rarely more than three, and arched over by the palmars and higher brachials, when these are present in the calyx, so as to be completely shut off from the plates of the tegmen. Tegmen elevated; its

plates heavy, and more or less turgid. Anal tube nearly central, very long, and gradually tapering. Arms simple, biserial, and very short. Confined to the Sub-Carboniferous of North America. Type—*B. icosidactylus*, Cassed.

Eretmocrinus, Lyon and Cassed. Like the preceding, but the *IR* of the dorsal cup continuous with those of the tegmen, and arms nearly twice as long; their upper portions much wider, spatulate, and folded inward. Anal tube shorter than in *Batocrinus*, and often bent abruptly to one side. Sub-Carboniferous; North America.

Dorycrinus, Roem. (Fig. 245). Calyx broadly turbinate or sub-globose, truncate at the base, and deeply sinuate in all the interradial areas, but chiefly so in the posterior one. Plates of the dorsal cup smooth or corrugated, but not striated, and all more or less convex. Tegmen strongly convex, composed of moderately heavy plates. Orals five, large; the posterior one nodose, or more frequently extended into a long spine, and occupying a central position. Surrounding these and overlying the ambulaera are five other spinous or nodose plates, which are separated by interradial pieces. Anus lateral in position, and

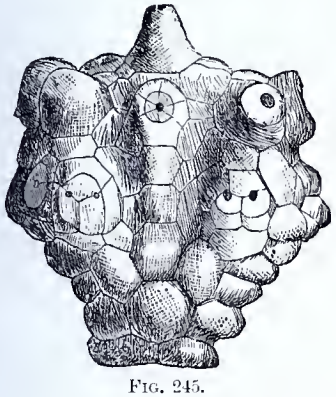


Fig. 245.

Dorycrinus quinquelobus, Hall, var. *intermedius*, M. and W. Sub-Carboniferous; Burlington, Iowa. Calyx viewed from the anal side. Natural size (after Meek and Worthen).

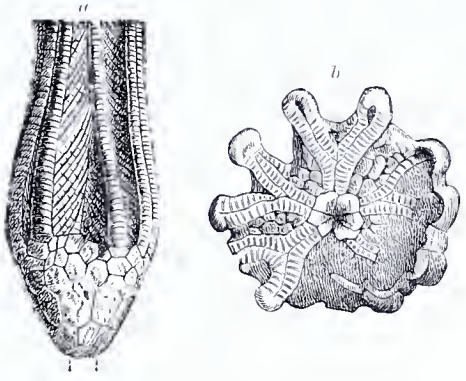


Fig. 246.

a, *Habrocrinus comtus*, Ang. Silurian; Gottland. Tegmen viewed from the anal side. Natural size; *b*, *H. ornatus*, Ang. Tegmen showing covering pieces of the ambulaera (after Angelin).

not extended into a tube. Arm openings twelve to twenty; the arm-bearing plates protubcrant. Devonian; Eifel. Lower Sub-Carboniferous; North America.

Agaricocrinus, Troost (Fig. 231). Calyx much depressed; basal disk flat or slightly concave. *R* supporting two primary *Br*, which are followed by short distichals, and in rays with more than two arms, by still shorter palmars. *IR* of the dorsal cup rarely more than four; those of the tegmen numerous, especially at the anal side. Tegmen high, pyramidal; the upper end occupied by a massive, button-shaped, central piece, which is surrounded by four similar, but slightly smaller plates; these constituting together the orals. Confined to the Sub-Carboniferous of North America. *A. Americanus*, Roem. sp.; *A. pentagonus*, Hall.

Alloprosalocrinus, Lyon and Cass. Warsaw Limestone.

Habrocrinus, Ang. (*Pionocrinus*, Ang.; *Carpocrinus*, Müll.), (Fig. 246). *B* three, equal. Costals 2×5; the distichals supporting the arms. *IRA* very large, and followed by numerous *IR*, arranged in rows of two or three plates. Arms uniserial, long, heavy, and simple throughout. Silurian; Gottland and England.

[The genus *Carpocrinus* was described by Müller as having no anal plate; but according to Angelin the type-species (*C. simplex*) has an *IRA* interposed between the radials. It must therefore be referred to *Habrocrinus*, which it resembles in all other respects.]

Fig. 247.

Desmidocrinus heterodactylus, Ang. Silurian; Gottland. Natural size (after Angelin).

Desmidocrinus, Ang. (Fig. 247). Like the preceding, but with a greater number of arms, which are longer, and composed of shorter joints. Silurian; Gottland.

Periechocrinus, Austin (*Geocrinus*, d'Orb.) Calyx large, elongate, somewhat urn-shaped, and composed of thin plates. *R* and primary *Br* long and narrow, frequently bearing a median longitudinal ridge. Distichals two; interradials very numerous, the second row composed of either two or three plates. Plates of the tegmen very small. Anal opening sub-central, sometimes prolonged in a tube composed of small, thin plates. Arms numerous, slender, branching, biserial; pinnules long and thin. Column round, pierced by an extremely large axial canal. Silurian; Gottland, England, North America.

Megistocrinus, Owen and Shum. Devonian to Middle Sub-Carboniferous; North America. *Abacocrinus*, Aug. Silurian; Europe. *Gennaeocrinus*, W. and Sp. Devonian (Hamilton Group): North America.

Family 4. **Barrandeocrinidae.** Angelin.

Base monocyclic. Basals three, enclosing an anal plate which supports three interradials. Arms biserial, recumbent; pinnules exposed, and directed upwards. Silurian; Gottland.

Barrandeocrinus, Ang. *R* followed by two costals; the upper ones giving off two heavy arms, which in perfect specimens are so closely folded as to conceal the calyx completely. Pinnules very long; their tips bending inward from opposite sides. Column cylindrical, and very heavy; axial canal circular. Silurian; Gottland.

[This genus is referred by Wachsmuth and Springer to the *Batocrinidae* and the family discontinued.]

Family 5. **Reteocrinidae.** Wachsmuth and Springer.

Monocyclic or dicyclic. Infrabasals, when present, five; basals four to five. Radials separated by a large IRA which supports a vertical row of higher anals all of nearly the same size; the upper ones passing gradually into the tegmen. The spaces to either side of this row, as well as the whole of the four other interrays, both in the dorsal cup and tegmen, paved with minute, irregularly formed pieces. Ordovician.

Reteocrinus, Bill. Calyx obconical; interradial and interaxillary areas profoundly depressed. *IB* five, differing considerably in size. *B* five, large, protuberant, hexagonal. *R* and fixed brachials forming a broad, highly elevated ridge, which passes insensibly into the arms. *IR* in contact with the *B*, and consisting of a large number of minute, irregular pieces. Tegmen composed of numerous, very small, convex plates, irregularly arranged. Arms with strong pinnules, and branching in the free state. Column sub-pentagonal. Ordovician; North America.

Xenocrinus, S. A. Miller. *IB* obsolete; *B* four; column quadrangular. Otherwise resembling *Reteocrinus*. Ordovician; North America.

Family 6. **Thysanocrinidae.** Wachsmuth and Springer.

(*Glyptocrinidae*, pp. Zittel; *Glyptasteridae*, Angelin.)

Base dicyclic. Radials laterally in contact, except at the posterior side, where they are separated by an anal plate. This is followed by several rows of interradials, between which additional anals are interposed. Ordovician and Silurian.

[*Thysanocrinidae* was substituted by W. and Sp. as a family name, on discovering the identity between *Glyptaster*, *Dimerocrinus*, *Eucrinus*, and *Thysanocrinus*. The last-named genus is entitled to priority, from being the first to have received a tolerably accurate description. *Glyptocrinus*, Hall, and *Stelidiocrinus*, Ang., are removed to the *Melocrinidae*.]

Thysanocrinus, Hall (*Glyptaster*, Hall; *Dimerocrinus*, Phill.; *Eucrinus*, Ang.) Calyx deep. *IRA* followed by three plates. Arms ten to twenty, biserial. Silurian (Niagara Group); North America, England, Gottland.

Hyptiocrinus, W. and Sp. Dorsal cup saucer-shaped, almost flat; the larger plates of the tegmen spiniferous. Arms pendent. Niagara Group; North America.

Ptychocrinus, W. and Sp. Like *Thysanocrinus*, but arms uniserial. Ordovician; North America.

Idiocrinus, W. and Sp. *IR* represented by a single large interbrachial in each of the interrays; that of the posterior side resting upon *IRA*. Niagara Group; North America.

Spyridiocrinus, Oehlert. Devonian; Saint Malo, France.

Lampterocrinus, Roem. Like *Thysanocrinus*, but having an anal tube; *IRA* large, and succeeded by three longitudinal rows of *IR*. Silurian (Niagara Group); North America.

Orthocrinus, Jaekel. Devonian; Rhineland.

Family 7. **Rhodocrinidae.** Roemer.

Base dicyclic. Infrabasals five; basals five, pentagonal, truncated at the upper end. The radials separated all around by large interradials. Anal area but very slightly, often not at all different from those of the other interrays. The rays generally free above the distichals; primary arms rarely more than ten, and either simple or branching. Pinnules long and closely abutting. Ordovician to Sub-Carboniferous.

Rhodocrinus, Miller (*Acanthocrinus*, Roem.) Calyx small, composed of delicate plates. *IB* frequently hidden by the column. *B* and *IR* large; the latter rapidly decreasing in size upward. Rays free from the distichals upward, and the ten primary arms branching once or oftener in the free state. Arms biserial, thin, and moderately short; pinnules closely crowded, long, and slender. Column round; axial canal stelliform. Ordovician to Middle Sub-Carboniferous; Europe and North America.

Archaeocrinus, W. and Sp. Calyx obovate. *IR* numerous, and enclosing a supplementary anal in the second or third row. Interdistichals generally present. Arms uniserial, branching. Ordovician; Canada.

Rhaphanocrinus, W. and Sp. Like the preceding, but with large *IB*, which are exposed in a side view. Arms long, simple, and uniserial. Ordovician; Ohio and Indiana.

Ollacrinus, Cumberl. (*Gilbertsocrinus*, Phill.; *Goniasteroidocrinus*, Lyon and Cassed.) Agreeing with *Rhodocrinus* in the structure of the calyx below the arms, but readily distinguished by the so-called pseudobrachial appendages, and by the size and disposition of the arms. Above each distichal is a round ambulacral opening (ten in all), through which the ambulacra of the arms conduct into the calyx. From above each of these openings spring two tufts of small, branching, pinnule-bearing arms. These are either folded over the tegmen, or they bend downwards with the ventral side exposed to view, the pinnules being directed upwards. Ten tubular appendages extend outwards and downwards from the upper margin of the calyx. In the American species these are united laterally in pairs for some distance; but in the European ones they are separated. One species in the Hamilton Group of New York; the remainder Sub-Carboniferous: North America and Europe.

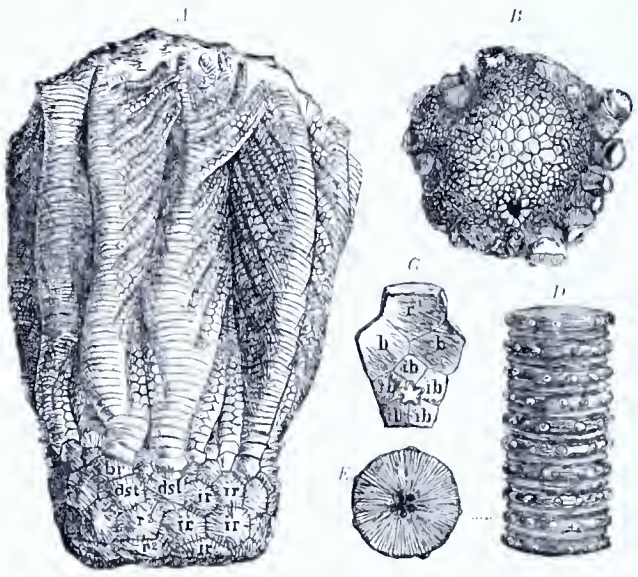


FIG. 248.

Rhipidocrinus crenatus, Goldf. sp. Devonian; Gerolstein, Eifel. *A*, Perfect crown, of the natural size (after Schultze). *B*, Tegmen, with eccentric anus. *C*, Interior view of the base, showing the five *IB*, two of the *B*, and one *R*. *D*, Column. *E*, Face of stem-joint.

Lyriocrinus, Hall. Calyx depressed; plates smooth or finely granulose. Tegmen almost flat, composed of a large number of small plates. Anus eccentric; not extended in an anal tube. Arms ten, strong, simple, biserial. Confined to the Niagara Group of North America.

Rhipidocrinus, Beyrich (Fig. 248). Calyx cup- or urn-shaped, with a more or less flattened or concave base. Plates of the dorsal cup heavy, and highly ornamented. *IB* five, small, forming a pentagon. *B* five, equal; *R* and axillary costals pentagonal. First *IR* large, heptagonal. Tegmen low, composed of an immense number of small thick plates, irregular in their arrangement; anus eccentric. Arms given off from calycular appendages, and composed of wide transverse pieces, which bear at intervals on alternate sides biserial, pinnule-bearing armlets. Column round, heavy; axial canal pentalobate. *R. crenatus*, Goldf. sp. Middle Devonian: Eifel.

Thylacocrinus, Oehlert. Resembling *Lyriocrinus*, but the calyx more elongate. *IR* and interdistichals profusely developed. Arms numerous, heavy, biserial, not branching in the free state. Devonian: France and North America.

Diamenocrinus, Oehlert. Devonian; Manche (France) and Germany.

Family 8. **Melocrinidae.** Zittel (emend. W. and Sp.)

Base monocyclic. Basals three to five; radials laterally in contact, not enclosing an anal plate. Interbrachials frequently separated by supplementary anals. Ordovician to Devonian.

Melocrinus, Goldf. (*Ctenocrinus*, Bronn), (Fig. 249). Calyx pyriform or melon-shaped, highly ornamented with radiating ridges or small nodules. *B* four; *R* hexagonal; *IR* numerous; those of the posterior interray enclosing one or more supplementary anals. Tegmen formed by relatively large, asymmetrical orals. Anal aperture eccentric, rarely extended in a small tube. Distichals of the same ray laterally united, either as far as the full length of the arms, or only for a short distance. They form in all five free calycular appendages, composed of single joints. From the outer sides of these appendages biserial, pinnule-bearing arms are given off at intervals in a lateral direction. Column round; axial canal small, round, or obtusely pentagonal. Silurian and Devonian; Europe and N. A.

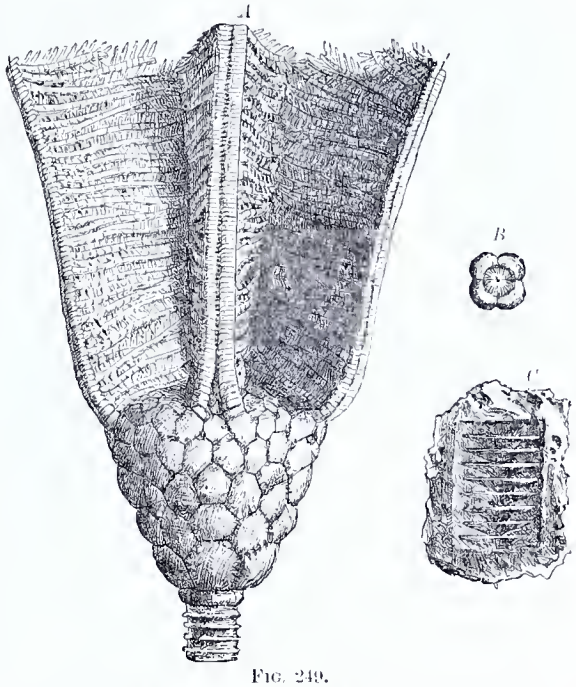


Fig. 249.

Ctenocrinus typus, Bronn. Devonian (Spiriferen-Sandstein); Daun, Eifel. *B*, Basals. *C*, Mould of stem-joints (the so-called "Schraubensteine").

Technocrinus, Hall. Like *Melocrinus*, but having strong, simple, uniserial arms, which do not bifurcate in the free state. Interbrachials not enclosing supplementary anals. Oriskany; Maryland.

Mariacrinus, Hall (emend. W. and Sp.) *B* four. Arms biserial, and given off directly from the calyx in an oblique direction. Surface ornamentation like *Glyptocrinus;* otherwise resembling *Melocrinus*. Silurian; Europe and North America.

Corymbocrinus, Ang. (*Polypeltes*, Ang.) Dorsal cup strictly pentamerous. *B* four, forming an inverted cup, and hidden beneath the column. Interbrachials large, not enclosing anal plates. Arms biserial, dichotomous, and closely apposed. Silurian; England and Gottland.

[The genus *Polypeltes*, Ang., is shown by Wachsmuth and Springer to have been founded upon erroneous observations, *P. granulatus*, Ang., being certainly a multibrachiate *Corymbocrinus*, in which the *B* and *R* are concealed in the inverted cup of the base. The family *Polypeltidae*, which was established by Angelin for the reception of this genus, is therefore discontinued.]

Patelliocrinus, Angelin (Fig. 242). Silurian; Gottland.

Scyphocrinus, Zenker. Calyx very large and elongate. Symmetry of dorsal cup slightly disturbed by anals which are interposed between the interbrachials. *B* four; distichals five or more; the lower palmars incorporated in the calyx, the upper ones free. Interbrachials very numerous. Arms biserial, long, branching. Silurian; Bohemia.

Glyptocrinus, Hall (Fig. 250). Dorsal cup obconical to sub-globose, ornamented with radiating striae passing from plate to plate; the elevations following the rays more pronounced, and forming well-defined rounded ridges, which meet imperceptibly with the free arm-plates. *B* five; interbrachials very

numerous, and enclosing supplementary anals, which sometimes form a continuous series. There are also numerous interdistichals, and frequently interpalmars, which form conspicuous depressions between the arm-plates. Tegmen low, composed of minute irregular pieces; anus eccentric. Arms ten to twenty, branching in the free state, long, slender, and uniserial. Column round, or exceptionally pentangular. Ordovician; North America.

Fig. 250.

Glyptocrinus decadactylus, Hall. Ordovician (Hudson River Group); Cincinnati, Ohio. Natural size.

Stelidiocrinus Ang. (*Harmocrinus*, Ang.) Form of dorsal cup as in the preceding, but the *IR* fewer and much larger, and plates generally without ornamentation. Plates of the tegmen also comparatively large. Arms uniserial, sometimes interlocking. Silurian; Europe and North America.

Macrostylocrinus, Hall. *B* three, unequal. Anal interradius much wider than the others; its first row of *IR* consisting of two interbrachials separated by a supplementary anal. The first row in the four other interrays consisting of a single interbrachial. Arms ten, simple, and biserial. Silurian; North America.

Allocrinus, W. and Sp. *B* three, unequal. Interbrachials few, longitudinally arranged. Arms uniserial. Silurian; North America.

Dolatocrinus, Lyon (*Cacabocrinus*, Hall). Dorsal cup perfectly pentamerous, cup-shaped or saucer-shaped. *B* primitively three, but completely anchylosed in the adult. Costals two; interbrachials few, the first ones extremely large. Tegmen comparatively flat, and composed of rather large plates, of which the orals form the summit. Anus at the end of a short tube. Arms biserial; generally branching. Devonian; North America.

Stereocrinus, Barris. Like the preceding, but the anchylosis of the *B* incomplete, and with only one costal. Hamilton Group; North America.

Family 9. **Calyptocrinidae.** Angelin.

Base monocyclic. Lower brachials and interbrachials forming an important part of the dorsal cup, which is perfectly pentamerous. Plates of the calyx limited to a definite number. Basals four; radials five, in contact all around; costals 2 × 5; *distichals two; and palmars* 2 × 10, *of small size. Arms twenty, resting in compartments formed by partitions attached to the tegmen.* Silurian and Devonian.

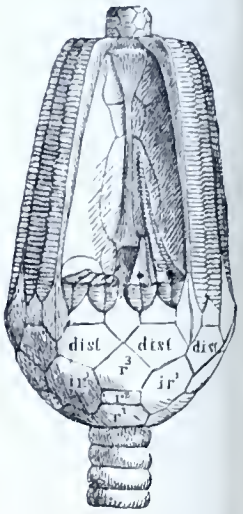


Fig. 251.

Eucalyptocrinus regularis, Hising. sp. Silurian; Gottland. Crown with arms removed from one ray in order to show the niches in which they repose.

Eucalyptocrinus, Goldf. (Figs. 251, 252). Calyx with a deep concavity at the lower end, the *B* forming the bottom, and the *R* the sides of an inverted cup. Supplementary pieces of the calyx consisting of 1 × 2 interbrachials, and one interdistichal; the latter of the same form as the interbrachials, and nearly as large as the two upper ones combined. Tegmen elongate, its upper part extended to form a tube. It is composed of five ranges of plates, of which the two middle ones are the least regular in their arrangement, and the upper one closes the centre. Attached to the outer walls of the tegmen, and extend-

ing to its top, are ten partitions supported by the interbrachials and inter-

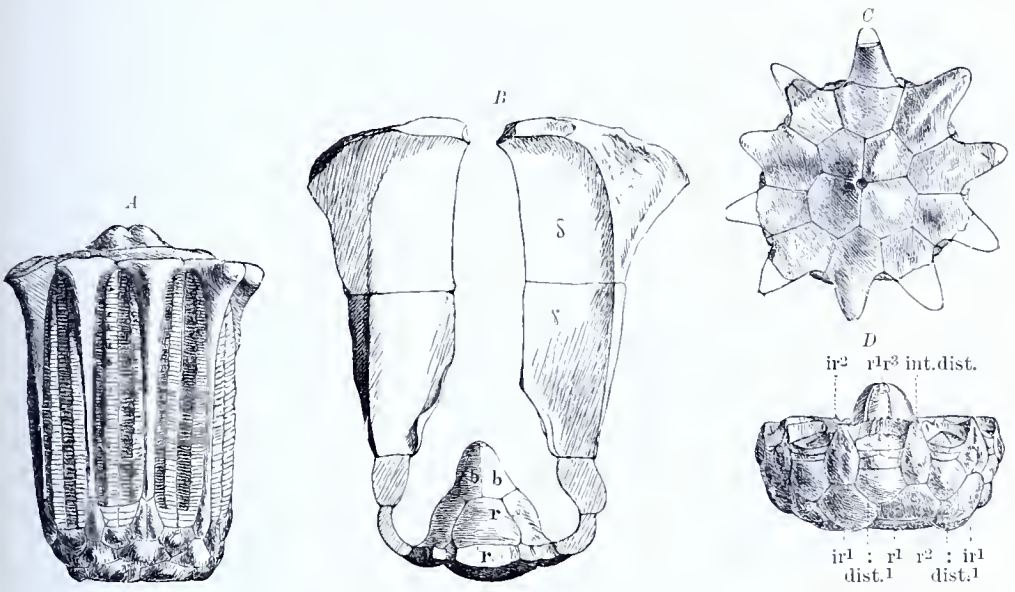


FIG. 252.

Eucalyptocrinus rosaceus, Goldfuss. Devonian; Gerolstein, Eifel. *A*, Perfect crown. *B*, Diagrammatic longitudinal section of the calyx (*b*, Basals; r^1, Radials; r^2, First costals; γ, Lower, and δ, upper piece of the wing-like processes). *C*, Tegmen. *D*, Dorsal cup (r^1, Radials; r^2, First costals; *ir*, Interradials; *dist.*, Distichals; *int. dist.*, Interbrachials, after L. Schultze).

distichals, which form deep, vertical compartments for the reception of two arms each. Arms twenty, biserial; composed of very narrow pieces. Column round. Silurian; Gottland, England (Wenlock Limestone), and North America (Niagara Group). A single species occurs in the Devonian of the Eifel.

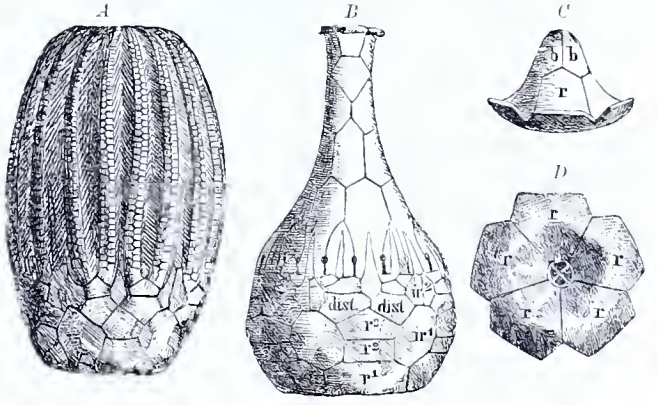


FIG. 253.

Callicrinus costatus, Hising. sp. Silurian; Gottland. *A*, Crown. *B*, Calyx showing the construction of the tegmen. *C*, Inner or ventral aspect of the base. *D*, Outer or dorsal aspect of the same. Natural size (after Angelin).

Callicrinus, Ang. (Fig. 253). Calyx flask-shaped; concavity at the base deeper and wider than in the preceding, sometimes involving not only the radials, but parts of the costals as well. Partitions for the reception of the arms much shorter, extending to less than half the height of the arms. Otherwise similar to *Eucalyptocrinus*, and sharing the same distribution.

Hypanthocrinus, Phill. Probably identical with *Eucalyptocrinus* (Fig. 251).

Family 10. **Crotalocrinidae.** Angelin (emend. W. and Sp.)

Base dicyclic. Dorsal cup composed of five infrabasals, five basals, five radials, an anal plate, and the lower brachials, which are laterally in contact. Upper edges of radials more or less excavated. Tegmen flat or but slightly elevated; its plates immovably

united by sutures. Orals asymmetrical; ambulacra bifurcating once or twice within the calyx, and roofed by two rows of very regularly arranged covering pieces; a few interambulacrals also present. Anus eccentric, placed at the end of a tube. Arms uniserial, dichotomising at short intervals throughout their entire length. Pinnules unknown. Column round, strong, the distal end formed into a thick root. Silurian.

This family embraces the genera *Crotalocrinus*, Austin (*Anthocrinus*, Müller), (Fig. 254), and *Enallocrinus*, d'Orb., both of which are found in the Silurian of Gottland and England.

The arms of the same ray are laterally united in *Crotalocrinus* throughout

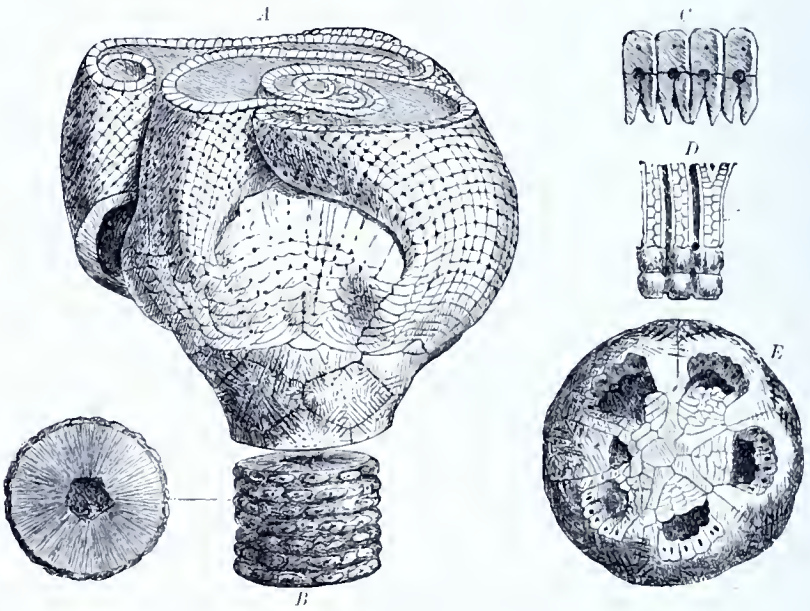


FIG. 254.

A, *Crotalocrinus pulcher*, Hising. (*Anthocrinus Loveni*, Müller). Silurian; Gottland. Crown with folded arms. *B*, Portion of stem. *C*, Cross-section of four contiguous arm-ossicles of the network. *D*, Dorsal aspect of arm-plates, showing their intimate union; those above the two rows figured have been broken away so as to expose the side-pieces and covering plates of the ambulacral furrows. *E*, Tegmen of *C. rugosus*, Miller (after Angelin).

their entire length, so as to resemble five broad, reticulate leaflets; while those of *Enallocrinus* are united for a certain distance only, and then become free. The arms in both forms were capable of being stretched out horizontally on the same level with the tegmen.

Order 3. FISTULATA. Wachsmuth and Springer.

(*Inadunata fistulata*, W. and Sp.; *Cyathocrinacea*, Neumayr.)

All plates of the dorsal cup united by close suture. Radials bisected or simple. Anal plate (IRA) generally, and radianal (RA) frequently represented; the former resting upon the truncated upper face of the posterior basal, the latter situated to the right of the IRA, and within the angle formed by the posterior and postero-lateral basals. Interradials proper not represented. Tegmen greatly extended at the posterior side to form an elongate or balloon-shaped sac. Ambulacra tegminal, lined by side-plates, and roofed over by small covering pieces. Mouth eccentric and subtegminal,

usually surrounded by five orals. Arms free from the radials upward; uniserial, or exceptionally biserial. Pinnules present or absent. Ordovician to Trias.

The *Fistulata* are characterised by an enormous development of the posterior interradius, which is extended upward so as to form a large *ventral sac* or *tube*. The plates of this sac are in some cases perforated by small, round, or slit-like pores (*respiratory pores*); while in others the pores are replaced by superficial pits. In the latter forms, a large, profusely perforated plate (*madreporite*) is interposed on the disk proper between the sac and the mouth.

The position of the anus, as observed by Wachsmuth and Springer, is at the side of the sac nearest the mouth; or it pierces the disk proper between the sac and the mouth.

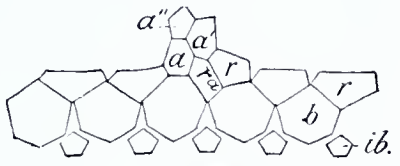


Fig. 255.

Diagram showing arrangement of plates in the dorsal cup of *Cromyocrinus*. *ib*, Infrabasals; *b*, Basals; *r*, Radials; *ra*, Radianal; *a*, *a'*, *a''*, Anal and lower tube plates (after Bather).

The radials in some families of the *Fistulata* are transversely bisected in one, two, or in three rays. When three of the compound radials are present, they are generally distributed in the right posterior, the anterior, and the left antero-lateral rays; but when only one radial is bisected, it is constantly that to the right of the anal area. The phases exhibited by the last-named plate in its palaeontological development furnish excellent differential characters. The superradial, or arm-bearing portion of the plate, is situated in the earlier forms directly in line with the inferradial or lower part of the plate; but in later forms it is pushed to the right by the gradual increase in width of the ventral sac. The inferradial remains constant in position, but when supporting the sac, as is usually the case among the later forms, it receives the name of *radianal*. Primitively, however, as was shown first by Wachsmuth and Springer, and subsequently by Carpenter and Bather, the radianal represents the lower portion of the right posterior radial; and it has, therefore, nothing in common with the anal plate, which is a specialised interradial.

Under the *Fistulata* are included the following families:—*Hybocrinidae*, *Anomalocrinidae*, *Heterocrinidae*, *Belemnocrinidae*, *Catillocrinidae*, and *Calceocrinidae*, comprising the monocyclic forms; and *Gasterocomidae*, *Cyathocrinidae*, *Poteriocrinidae* [*Encrinidae*], and *Agassizocrinidae* among the dicyclic.

Family 1. **Hybocrinidae.** Zittel.

Base monocyclic. Basals five, high. The right posterior radial compound; the inferradial supporting the ventral sac; the superradial extremely small or undeveloped. Ventral sac in its most primitive form, extending but little above the rest of the tegmen. Ordovician.

Hybocrinus, Billings. Calyx cup-shaped or obconical. Inferradial large, angular above; supporting to the right a very small superradial, and to the left the first tube-plate, which generally resembles the superradial in form and size. *R* with a crescent-shaped facet. Arms simple, devoid of pinnules, and composed of quadrangular joints. Ordovician; Canada, Kentucky, and Tennessee.

Hoplocrinus, Grewingk (Fig. 256). Like the preceding, but with the inferradial sloping only to the right, and supporting a small, trigonal super-

radial. On the left it supports small plates of the ventral sac, without the intervention of a larger plate. Ordovician; St. Petersburg.

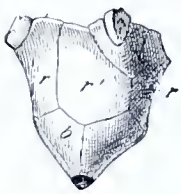


Fig. 256.

Hoplocrinus dipentas, Grewingk. Ordovician; St. Petersburg. Calyx seen from the anal side (after Grewingk).

Hybocystes, Wetherby. Arrangement of calycine plates the same as in *Hybocrinus*, but differing in the arm structure. Three of the rays bearing primitive arms composed of but few joints; ambulacral furrows passing from the ventral to the dorsal side of the arms, and continued upon the surface of the *R*. The two other rays are without arms, and the ambulacra follow the surface of the calyx, passing down so far as to enter the basals. Ordovician; Kentucky.

Bucrocrinus, Volborth. Like *Hoplocrinus*, but the right posterior and the anterior ray without arms; apparently inferradials only are developed. Ordovician; St. Petersburg.

Family 2. **Anomalocrinidae.** Wachsmuth and Springer.

Base monocyclic. Radials very irregular in form, the right posterior and left antero-lateral ones compound, all of them laterally in contact. Ventral sac small, tubular; its lowermost plate resting in the angle formed by the superradial to the right, and the upper end of the simple radial to the left. Arms uniserial, bifurcating at intervals. Pinnules or small armlets given off from each arm-joint on one side only, as far as from one bifurcation to the next, when they change to the opposite side. Ordovician.

Anomalocrinus, M. and W. *B* five. Unique in that the large simple *R* of the posterior ray is often longitudinally bisected in the median line. A small quadrangular supplementary piece enclosed within the basal ring. Tegmen composed of large plates. Column strong. Ordovician; North America.

Family 3. **Heterocrinidae.** Zittel (emend. W. and Sp.)

Base monocyclic; basals five; one or more of the radials compound. The inferradial of the right posterior ray supporting to the right the superradial, and to the left the ventral sac. Anals absent. Arms uniserial. Ordovician and Silurian.

Heterocrinus, Hall (*Stenocrinus*, W. and Sp.) Crown sub-cylindrical, calyx small, arms long. Three of the *R* compound; the others simple, and shorter. The inferradial of the posterior ray has the form of an axillary, supporting to the left the ventral sac, and to the right the superradial. Arms comparatively stout, giving off long branchlets at intervals, which often branch again. Column very large, pentagonal, and quinquepartite; the lines of suture interradial in position. Ordovician; North America.

Ectenocrinus, S. A. Miller (*Heterocrinus*, W. and Sp. non Hall). Like the preceding, but the arms formed of continuous series of syzygies comprising two plates each, the epizygals giving off long armlets. Column of moderate size, round, and tripartite; axial canal large and pentalobate. Ordovician; North America.

Ohiocrinus, W. and Sp. Differs from *Heterocrinus* in the details of its arm-structure, and in the form of the ventral sac. Arms ten, long, and giving off from every third or fourth joint long filiform armlets, which extend to the full height of the main arms. Ventral tube resting upon the left sloping side of the right posterior inferradial (*RA*), and ascending spirally with the adjacent

convolutions in contact. Column strong, obtusely pentagonal, and quinquepartite. Ordovician; North America.

Iocrinus, Hall. *B* five, small; *R* five, the right posterior one compound. The lower section of the latter, which serves as radianal, nearly of the same size as the other *R*, but angular above instead of concave. It supports the superradial on the right, and the ventral sac on the left; it is so large as to extend considerably above the level of the other *R*, thus assuming the aspect of an axillary brachial. Ventral sac composed at its posterior side of a longitudinal row of large, solid, elongate plates; at the other sides of short, delicate, transverse pieces; the former plates being attached to the *RA*, are easily mistaken for arm ossicles. Arms without pinnules, branching. Column sharply pentagonal; the angles radially disposed. Ordovician; North America.

Herpetocrinus, Salter (*Myoleductylus*, Hall). *B* five, of irregular form and size. *R* five, the right posterior one horizontally divided. Ventral tube long and narrow, and resting upon the sloping upper face of the inferradial. Arms non-pinnulate, branching. Column evolute at its upper end, and more or less round; involute and crescent-shaped toward the terminal end, with large cirri springing from the two horns of the crescent; section sharply pentagonal. Silurian; North America and Europe.

Family 4. **Belemnocrinidae.** Wachsmuth and Springer.

Base monocyclic; cylindrical to ovoid. It is composed of five large, elongate, irregular pieces, and is pierced by a small canal which widens slightly at the upper end. Radials five, quadrangular, and separated posteriorly by a narrow IRA. Ventral sac large, composed of hexagonal plates, the angles of which are perforated. Arms long, giving off armlets alternately at intervals. Column round or pentagonal; in the latter case having its angles radially directed. Cirri, when present, interradial in position. Sub-Carboniferous.

Belemnocrinus, White. Burlington Group; Mississippi Valley.

Family 5. **Catillocrinidae.** Wachsmuth and Springer.

Base monocyclic; dorsal cup saucer-shaped; general symmetry of the calyx greatly disturbed. Basals irregular in form, their number unknown; radials still more irregular both in form and in size. Most of the arms given off from two of the radials, which are sometimes five or six times larger than the other three; they are simple, quadrangular, and rest within small sockets directly upon the radials. Anal plates wanting. Ventral tube heavy, composed of very long, longitudinally arranged crescent-shaped pieces, and supported directly by the radials; it exhibits a wide open groove along the anterior side, which probably was covered by small delicate plates. Devonian and Sub-Carboniferous.

Catillocrinus, Troost. Crown, when the arms are closed, elongate, cylindrical. Calyx basin-shaped, concave at the base, truncate at its upper margin. Basal disk small. *R* five; those of the two antero-lateral rays fully six times as wide as the others, and expanding upwards, so as to encroach upon the smaller ones. The larger *R* support twelve to sixteen arms; the smaller ones rarely more than one each. Sub-Carboniferous; North America.

Mycocrinus, Schultze. Dorsal cup mushroom-shaped. Plates massive, irregular, and without ornamentation. *B* two (according to Schultze), one of

them twice as large as the other, and the two forming a knob-like body. *R* five, their inner edges resting upon the angular margin of the basal disk; they spread broadly outward from the *B*, extending far beyond them. The two larger *R* separated at the posterior side by two equal smaller plates; and at the anterior side by a single plate having a quite narrow upper face. *M. boletus*, Schultze, apparently with fifteen arms; their structure unknown. Middle Devonian; Eifel.

Family 6. **Calceocrinidae.** Meek and Worthen.

"*Inadunata Monocyclica, in which a bilateral symmetry along the left anterior radius and right posterior interradius has been superinduced in conjunction with bending of the crown on the stem in such a way that the right posterior interray lies along the stem; with the left anterior, right posterior, and right anterior radials compound; with anal x (IRA) shifted over the right posterior radius, usually into the right posterior interradius, and supporting a massive tube; with three, rarely four arms, of which two are as a rule peculiarly modified and bear armlets or pinnules.*"—*Bather*, The Crinoidea of Gotland. Ordovician to Sub-Carboniferous.

Castocrinus, Ringueberg. *B* distinct, all entering into the articular surface of the stem. The right posterior, and right antero-lateral superradials joined by ill-defined close suture, each abutting with one side on the adjacent large simple *R*. The lower plate of the tube supported by the right posterior superradial only, while the right antero-lateral superradial supports the first brachial of the right antero-lateral arm. The right posterior and right antero-lateral superradials separated from one another, and also from the ventral tube, by the right posterior and right antero-lateral *R*. Arms four. Ordovician; North America. Type, *C. furcillatus*, W. R. Billings sp.

Euchirocrinus, M. and W. *B* unfused, or perhaps sometimes the left posterior fused with the left antero-lateral one. The right posterior and right antero-lateral superradials fused in a T-shaped piece, which abuts with either wing on the corners of the large simple *R*. The right posterior and right antero-lateral inferradials separated from one another and from the tube by the T-piece; tube supported by the whole upper margin of the latter. Arms three. Ordovician and Silurian; North America. Type, *E. punctatus*, Ulrich sp.

Calceocrinus (Hall) Ringueberg. Left posterior *B* fused with the left antero-lateral one; the fused plates very rarely entering the stem articulation. The posterior and right antero-lateral *B* bounded for some distance by the large *R*. T-plate separated from the large simple *R* by the right posterior and right antero-lateral *R*; it is low, wide, and occasionally very small. Tube supported by the T-piece and the two inferradials to the right, but not touching the two large simple radials. Arms three. Silurian and Devonian; Europe and America. Type, *C. typus*, Ringueberg.

Halysiocrinus (Ulrich) Bather. *B* as in the preceding, but the fused posterior and right antero-lateral ones never entering into the stem articulation. T-piece either obsolete or concealed between the right posterior and right antero-lateral inferradials, and the two large *R* in the stem articulation. Tube supported by the inferradials to the right, which are in contact; and abutting by its lower corners on the two large simple *R*. Arms three. Burlington and Keokuk Groups; Mississippi Valley. Type, *H. ventricosus*, Hall sp.

Family 7. **Gasterocomidae.** Wachsmuth and Springer.

Base dicyclic. Infrabasals anchylosed into an undivided disk, which is pierced by a large quadrilobate canal. Radials large; articular facets directed outward, horseshoe-shaped, occupying nearly the whole outer face of the plates, and pierced by a large dorsal canal. Anal opening low down, situated directly above the anal plate and between two radials. Tegmen composed of five interradials, five orals, and ambulacral plates. Devonian.

Gasterocoma, Goldf. (*Epactocrinus*, Müller), (Fig. 257). Infrabasal disk extending but slightly beyond the eolumn; surrounded by five *B*, of which the posterior one is slightly truneated. *R* five, three of them equal, the two posterior ones irregular; the latter enelose the *IRA* and anal opening, whieh is surrounded by a few small pieees. The arms, as indieated by the charaeter of the radial faeets, either reeumbent or widely divergent. Devonian; Eifel.

Fig. 257.

Gasterocoma antiqua, Goldf. Devonian; Prüm, Eifel. *a*, Calyx seen from one side; *b*, Anal aspect; *c*, Tegmen. $^2/_1$ (after L. Schultze).

Nanocrinus, Müller. Similar to the preeeding, but only four of the *R* arm-bearing. The right antero-lateral one, however, has two artieular facets, and evidently supported a pair of arms instead of a single one; the anterior *R* is eonsiderably smaller, and has no artieular faeet. Devonian.

Achradocrinus, Schultze; *Scoliocrinus*, Jaekel. Devonian; Germany.

Family 8. **Cyathocrinidae.** Roemer (emend. Wachsmuth and Springer.)

Base dicyclic. Radials simple or compound; their upper edges furnished with a small crescent-shaped facet. Radials and arm-plates united by close suture, as are the latter among each other. IRA usually, and RA occasionally present. Tegmen with five orals and a madreporite, extended into a strong ventral tube. The disk ambulacra resting on the lateral margins of two large interradial plates; they are lined by side-pieces, and roofed over with covering plates. Arms without pinnules, long, branching, and uniserial. Ordovieian to Carboniferous.

Dendrocrinus, Hall (? *Palaeocrinus*, Billings). Calyx obeonieal, higher than wide, unsymmetrieal. *IB* five, equal. *B* five, the largest plates in the ealyx; the posterior one truncated at its upper faee, and supporting a large anal plate. Four of the *R* pentagonal and simple; the right posterior one eompound, with the two parts vertically arranged. *IRA* sueceeded by two or three plates whieh form the base of the ventral sac, but are partly enelosed in the ealyx. Ventral sae very large. Arms long and braneliing; eolumn sharply pentagonal, or sub-pentangular. A number of speeies oeeur in the Ordovieian of North Ameriea, but only a single doubtful one known from the Silurian (Niagara Group).

Homocrinus, Hall (Fig. 258). Like the preeeding, exeept that the arm-bearing portion of the right posterior radial is pushed over toward the right, so as to support, eonjointly with the anal, the ventral sae. Silurian; North Ameriea. Devonian; Rhineland.

Gastrocrinus and *Rhadinocrinus*, Jaekel; *Bactrocrinus*, Stein. Devonian.

Cyathocrinus, Miller, emend. W. and Sp. (Figs. 259, 260). Dorsal cup cup-shaped, bilaterally symmetrical. *IB* five, equal. *B* large; the posterior one truncated for the support of an anal plate. *R* five, all simple; their upper faces provided with a facet occupying less than the full width of the plates. Ventral sac rarely extending to more than one-half the height of the arms. The number of costals extremely variable among the rays. Arms rather delicate, composed of elongate cylindrical joints, and giving off numerous branches, most of which divide again. Column round. Ordovician to Sub-Carboniferous; Europe and North America.

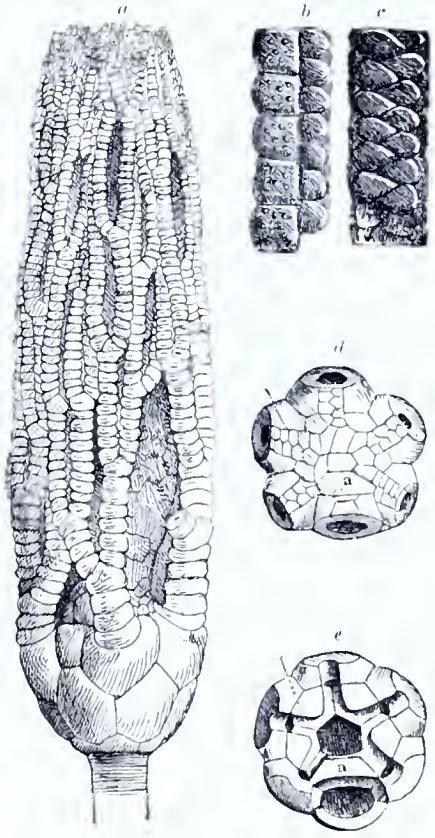


Fig. 260.

a, *Cyathocrinus longimanus*, Ang. Silurian; Gottland. Crown of the natural size (after Angelin); *b*, *C. ramosus*, Ang. Portion of an arm viewed from the side; *c*, Ventral aspect of same (enlarged); *d*, *C. malvaceus*, Hall. Sub-Carboniferous; Burlington, Iowa. Tegmen perfectly preserved; *e*, The same after removal of the covering pieces and orals (after Meek and Worthen).

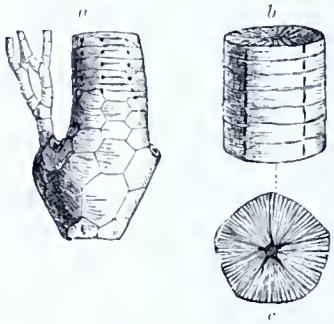


Fig. 258.

Homocrinus curtus, Müll. sp. Devonian; Schöneeken, Eifel. *a*, Calyx from the anal side, showing ventral sac and one arm (right and left sides reversed); *b*, Stem; *c*, Face of stem-joint (after Schultze).

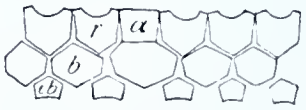


Fig. 259.

Cyathocrinus. Diagram of dorsal cup (after Bather).

Lecythocrinus, Müller, emend. Zittel (Figs. 225, 261).[1] Like the preceding, except that the infrabasals are very small, and entirely concealed by the column. Ventral sac in the form of a long tube, and composed of numerous, very regularly arranged hexagonal plates. Column obtusely quadrangular, composed of long joints, and perforated by a large central and four peripheral canals. Devonian; Eifel.

Gissocrinus, Ang. (Fig. 262). *IB* three to five. *B* five; the posterior one truncated, and supporting an anal plate. Radial facets elliptical in contour. Ambulacra roofed over by alternately arranged covering pieces. Ventral sac long, always laterally folded. Madreporite well defined. Arms long, regularly bifurcating. Silurian; Gottland and England. Devonian; Eifel.

Arachnocrinus, M. and W. Calyx very small, resembling *Cyathocrinus* in the arrangement of its plates, but forming a bulbous protuberance from which the robust arms stretch out horizontally. Silurian and Devonian; Europe and North America.

[1] [The type-specimen upon which this genus was founded (*L. Eifelianus*, Müll.) was regarded by Schultze as an abnormal variety of *Taxocrinus*, and the specific name was changed by him to *T. briareus*. But *Taxocrinus* has no such ventral tube, nor has it peripheral canals. In the latter respect *Lecythocrinus* differs also from *Gissocrinus*, with which it otherwise has close affinities.]

Mastigocrinus, Bather. Probably merely a variety of *Cyathocrinus*, with which it agrees in structure of the calyx and mode of branching. The arms, however, are relatively longer, as is also the ventral tube; column quinquepartite. Silurian; Dudley, England.

Botryocrinus, Ang. Calyx small, cup-shaped, unsymmetrical. *IB* five, high, slightly protuberant. *B* five, three of them hexagonal and equal; the posterior pair indented by the radianal. *R* five, very large, with excavated facets. *RA* small, rhomboidal, and supporting the ventral sac. Arms ten, giving off armlets from alternate sides of each or of every second or third joint throughout their entire length; in some species the armlets give off subbranches. Ventral sac in the form of a tube which coils upon itself like a snail at about one-fourth the height of the arms. Anal opening situated anteriorly at the base of the tube. Silurian; Gottland.

Barycrinus, Wachsm. Differs from *Cyathocrinus* in having massive arms,

Fig. 261.

Lecythocrinus Eifelianus, Müll. Devonian; Eifel. Restored (after Schultze).

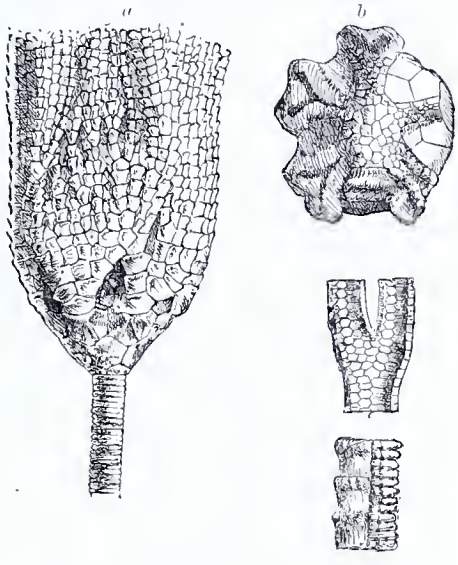


Fig. 262.

a, *Gissocrinus arthriticus*, Phill. Silurian; Gottland. Crown of the natural size (after Angelin); *b*, *G. punctuosus*, Ang. Tegmen; *c*, Ventral and lateral aspect of the arms (enlarged).

composed of rather short, heavy, almost circular pieces, and exhibiting very narrow ambulacral furrows. In some species the *IRA* sustains a diminutive supplementary piece to the right, which is wanting in others. Ventral sac composed of but few rows of heavy plates, longitudinally arranged. Column stout, obtusely pentagonal, and quinquepartite; axial canal very large. Sub-Carboniferous; North America.

Euspirocrinus, Ang. (Fig. 219). Dorsal cup conical, composed of massive plates. *IB* five; *B* five; *R* with a deep and broad articular facet, notched for the passage of the axial cord. *IRA* large, rising above the level of the *R*. Radianal somewhat smaller, and supporting a plate of the ventral tube which takes part in the dorsal cup. Tube cylindrical, composed of relatively large plates. Tegmen formed of five interradial pieces, which support by their lateral edges two rows of side pieces enclosing an irregular row of covering plates. Madreporite small; column quinquepartite. Silurian; Gottland.

Streptocrinus, W. and Sp. (*Ophiocrinus*, Ang. non Salter nec Semper). Plates of the dorsal cup as in *Cyathocrinus*. Ventral sac composed of about eight rows of hexagonal plates, some of which are deeply folded transversely, so as to produce well-marked depressions on the surface. Arms slightly bending downward; their ambulacral grooves narrow, and provided with covering pieces only. Silurian; Gottland.

Tenarocrinus, Bather. Dorsal cup broad, and composed of thin plates; the truncated posterior *B* supporting a large *IRA*. The right posterior *R* compound; its superradial shifted to the right; but the inferradial, notwithstanding its slanting position, gives no support to the ventral sac. The latter is very large, longitudinally folded, and covered with transverse rows of pits. Column round, with very wide axial canal. Silurian; Dudley, England.

Parisocrinus, W. and Sp. Dorsal cup obconical, composed of five *IB*, five *B*, and five *R*, with an anal and radianal; the latter two together supporting the long, cylindrical, ventral sac. Upper edges of the *R* excavated so as to form a narrow semicircular facet for the reception of the first costals; number of the latter very variable among the rays. Arms multibrachiate, divergent, and filiform at their tips. Column round. Devonian; Germany. Sub-Carboniferous: North America.

Atelestocrinus, W. and Sp. Dorsal cup elongate, always more or less constricted along the suture line between the basals and infrabasals. *IB* five, large, forming an almost solid ovo-cylindrical body. *B* five, long and narrow; *R* five; four of them equal and arm-bearing, the anterior one less than half the size of the others and not arm-bearing. Costals 4 × 4, the uppermost axillary, and supporting two main arms; armlets given off on alternate sides from every second plate. Anal interradius as in the preceding. Burlington and Keokuk Groups; Mississippi Valley.

Sphaerocrinus, Roemer, and *Achradocrinus*, Schultze. Of these only the structure of the calyx is known. The dorsal cup in both forms is globular, composed of very thin plates, and the arms are pierced by a dorsal canal. In the first-named genus *IRA* and *RA* are both represented, and it has an eccentric anal opening which is directed upwards. But in the second *RA* is wanting, and the position of the anus is strictly lateral, it being situated in the suture line between the posterior radials. Middle Devonian; Eifel.

Codiacrinus, Schultze. Calyx small, resembling a poppy head. *IB* five; *B* five; *R* five; the plates within each circlet equal to one another, and laterally in contact. Devonian; Germany.

Lecythiocrinus, White. Arrangement of calyx plates as in the preceding, but with wider radial facets; these are directed upwards instead of obliquely outwards, and are provided with transverse ridges and well-defined ligamentous fossae. Coal Measures; North America.

Family 9. **Poteriocrinidae.** Roemer.

Base dicyclic. Infrabasals five, sometimes hidden by the column. Basals five; radials five, with transverse articular ridges. Anal and radianal generally represented; and lower plates of the tube frequently entering into the dorsal cup. Ventral sac large; elongate or balloon-shaped in the earlier forms, small and conical in the later ones; it is composed of hexagonal plates, having the angles perforated by pores.

Arms simple or branching, uniserial, interlocking, or occasionally biserial, and all having large pinnules. Devonian and Carboniferous.

Poteriocrinus, Miller. Dorsal cup obconical; plates thin and plicated around their margins so as to form triangular pits at the angles. *IB* equal; *B* high. Three of the *R* hexagonal; the posterior and the right postero-lateral ones

Fig. 263.

Scaphiocrinus unicus, Hall. Sub-Carboniferous (Keokuk Group); Crawfordsville, Indiana. Natural size.

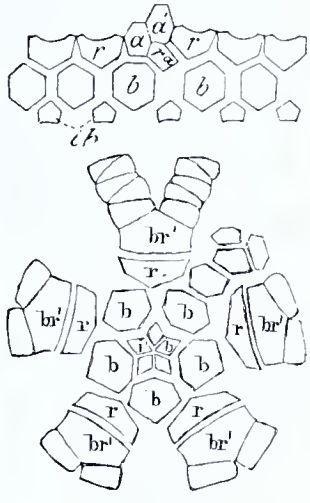


Fig. 264.

Diagram showing arrangement of plates in the dorsal cup of *Scaphiocrinus*.

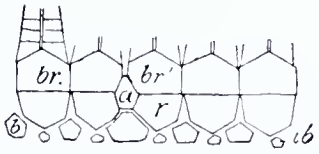


Fig. 266.

Diagram of *Graphiocrinus*. *ib*, Infrabasals; *b*, Basals; *r*, Radials; *a*, Anal; *br*, Brachials (after Bather).

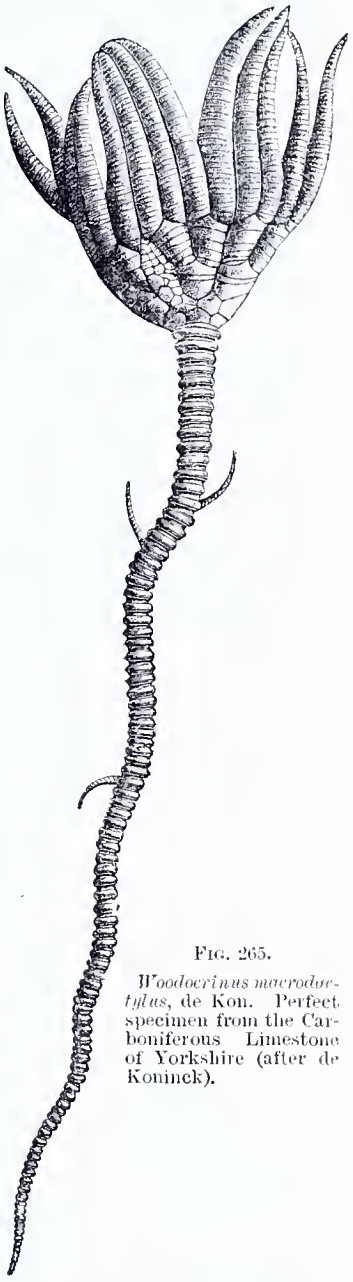


Fig. 265.

Woodocrinus macrodactylus, de Kon. Perfect specimen from the Carboniferous Limestone of Yorkshire (after de Koninck).

heptagonal, and rising above the level of the others. Articular facets crescent-shaped, and rarely occupying the full width of the plates. Anal and radianal both present. Ventral sac very large, tubular, and extending to the full length of the arms; its two lowermost plates partially incorporated into the sac. Arms long, branching, composed of cuneate joints, alternately arranged. Column round or obtusely pentagonal. Upper Devonian and Sub-Carbon.

Lophocrinus, v. Meyer. Devonian; Nassau.

Scaphiocrinus, Hall (*Hydriocrinus*, Trautsch.), (Figs. 263, 264, 269). Dorsal cup low cup-shaped to saucer-shaped. Arrangement of plates and mode of articulation as in the preceding; but the upper faces of the *R* form a horizontal line, and are completely occupied by the lower faces of the first brachials. Costals one or two; the axillaries provided with transverse ridge and fossae similar to

those of the *R.* Arms long, uniserial, branching, and composed of wedge-shaped joints, alternately arranged. Sub-Carboniferous and Coal Measures.

Scytalocrinus, W. and Sp. Dorsal cup generally deep. Arrangement of calyx plates as in the preceding, from which it differs in the character of the arms. These are stronger, and remain undivided after the first bifurcation, which takes place above the first or second brachial. They are straight, and composed of moderately short, very slightly wedge-shaped joints. Pinnules long and rather closely abutting. Sub-Carboniferous.

Decadocrinus, W. and Sp. Dorsal cup very short, concave at the bottom. Arrangement of plates of the dorsal cup as in the preceding, but the arms simple and thinner, and composed of long, decidedly cuneate joints, which give them a strongly waving or zigzag outline. Pinnules very robust, closely resembling armlets, and widely separated. Sub-Carboniferous; North America.

Woodocrinus, de Kon. and le Hon (*Philocrinus*, de Kon.; *Pachylocrinus*, W. and Sp.), (Fig. 265). Dorsal cup saucer-shaped. *IB* five, small, generally covered completely by the column. *B* large, their lower portions curving inward together with the *IB*, and forming a concavity. Anal area and mode of articulation as in *Scaphiocrinus*. Ventral sac short, bulging toward the upper end. Arms twenty or more, uniserial, heavy, and closely folded so as to be laterally in contact; arm-ossicles very short. Pinnules long and numerous. Column round. Sub-Carboniferous; England and North America.

Zeacrinus, Hall (Troost). Resembling *Woodocrinus* in form and construction of the dorsal cup, but with short, thick, sub-pyramidal ventral sac. *IRA* and *RA* both present; the latter especially large, and deeply inserted between the *B*. Arms short, uniserial; the two main divisions of each ray giving off numerous branches toward the inner side. These branches fit so closely together that when the arms are closed the crown appears like a perfectly solid body. Arm-ossicles short, transversely arranged. Middle and Upper Sub-Carboniferous.

Coeliocrinus, White, and *Hydreionocrinus*, de Kon., are closely related to *Woodocrinus* and *Zeacrinus*. They are distinguished chiefly by the form of the ventral sac, which in *Coeliocrinus* is balloon-shaped, and in *Hydreionocrinus* mushroom-shaped. They are found in the Lower and Upper Sub-Carboniferous respectively.

Graphiocrinus, de Kon. and le Hon (Fig. 266), and *Bursacrinus*, M. and W., differ from the majority of the *Poteriocrinidae* in having but one anal plate, *RA* being absent. Dorsal cup depressed, concave at the bottom; *IB* very small, generally covered by the column. *Graphiocrinus* has ten main arms, which are simple; and the ten main arms of *Bursacrinus* give off branches in a similar fashion as in *Zeacrinus*. Sub-Carboniferous; North America.

Miller and Gurley describe under *Aesiocrinus* a Carboniferous form agreeing with *Graphiocrinus* in the construction of the calyx; but the plates of the ventral sac are extremely heavy, and enclose a narrow cavity; while the plates of the sac in the typical form are rather delicate, and the inner space is relatively wider.

[In addition to the above, the following genera have also been associated with the *Poteriocrinidae*:—*Cromyocrinus*, *Phialocrinus*, and *Stemmatocrinus*, Trautsch.; *Eupachycrinus* and *Erisocrinus*, M. and W.; *Ceriocrinus*, White; and *Ulocrinus*, Miller and

Gurley. Although agreeing with this family in a general way, they are readily distinguished from the typical forms by certain characters which they possess in common with the *Encrinidae*. The dorsal cup is saucer-shaped, and composed of heavy plates; the articular faces of the radials are provided with well-marked muscular fossae; the arms vary from uniserial to biserial within the limits of the same genus; and the ventral sac is reduced to a small cone, extending but little above the level of the ventral disk.

These genera, according to Wachsmuth and Springer, constitute, together with the genus *Encrinus*, a group which is sufficiently distinct to be recognised as an independent family.

European writers, on the other hand, have almost without exception agreed in associating *Encrinus* in the same category with recent Crinoids; the reasons for this being partly because it is a Mesozoic form, partly because it has axial canals along the inner floor of the dorsal cup, and, finally, because anal plates are wanting. But the imaginary line which was formerly conceived as separating the Palaeozoic from the Neozoic Crinoids, has now been generally abandoned; and as axial canals have been found to exist among Palaeozoic forms as well as among the later ones, the only vital distinction remaining is the presence or absence of anal plates.

In point of fact anals are present in most of the above-named genera. *Cromyocrinus* and *Eupachycrinus* have both an *RA* and *IRA*; *Phialocrinus* has only the *IRA*, and *Ulocrinus* only the *RA*; but *Stemmatocrinus* and *Erisocrinus* agree with *Encrinus* in having neither *IRA* nor *RA*. Hence, if the division between the *Poteriocrinidae* and *Encrinidae* be established simply upon the presence or absence of anal plates in the cup, *Stemmatocrinus* and *Erisocrinus* are necessarily included under the latter family, and the remainder excluded. But if other characters be chosen as criteria, such as the mode of articulation, and the reduction of the ventral sac, then all of the above genera must be included in the same family with *Encrinus*. The latter course appears preferable; especially since the gradual disappearance of anals may be regarded as a natural consequence of the decrease in size of the ventral sac. Adopting this course, the family *Encrinidae* may be defined as follows:—

Calyx more or less saucer-shaped, with dicyclic base. Infrabasals five, small, generally concealed beneath the top stem-joint. Articular faces of the radials forming a horizontal line, and completely occupied by the first costals; faces provided with large muscular fossae, and a perforated transverse ridge. Costals one or two. Ventral sac rudimentary; anal plates generally absent. Tegmen (in Encrinus) elevated, composed of rather heavy plates. Arms usually ten, rarely five or fourteen; pinnule-bearing. Carboniferous and Trias.]

Cromyocrinus, Trautsch. (Fig. 267). Dorsal cup low, cup- or saucer-shaped. *IB* moderately large, always projecting beyond the column. *IRA* large; *RA* barely touching the ventral sac; no plates of the latter entering the dorsal cup. Costals one to each ray. Arms ten, rarely five; uniserial or slightly interlocking from opposite sides. Column round. Carboniferous Limestone; Moscow, Russia. Kaskaskia Group; Mississippi Valley.

Fig. 267.

Cromyocrinus globulus, M. and W. Sub-Carboniferous; Chester, Ill. Natural size (after Meek and Worthen).

Eupachycrinus, M. and W. Dorsal cup as in the preceding genus, but the *IB* much smaller, and concealed by the column. *B* large. *IRA* and *RA* both represented; the latter very large, and supporting a small plate of the ventral tube, the lower part of which descends into the cup. Arms generally ten, rarely five or fourteen; either uniserial, interlocking, or biserial. Kaskaskia Group; Mississippi Valley.

Ceriocrinus, White (*Delocrinus*, Miller and Gurley). Dorsal cup as in the preceding, but the posterior *B* more elongate than the others, and supporting a small *IRA*; upper end of the latter extending above

the *R*. Radianal wanting. Costals one or two; the lower one frequently extended into a spine. Arms ten, short and heavy, uniserial or biserial. Kaskaskia Group and Coal Measures; Mississippi Valley.

Phialocrinus, Trautsch. Construction of anal area as in *Graphiocrinus*, but the mode of articulation between radials and brachials as in *Encrinus*. Ventral sac small. Costals two; arms ten. Accompanies the preceding, and found also in Carboniferous Limestone of Russia.

Ulocrinus, Miller and Gurley. Dorsal cup globular or cup-shaped. *IB* projecting beyond the column. *B* large; the posterior one variable in size, but hexagonal like the others. *IRA* absent; *RA* large, occupying the full height of the *R*, and supporting the ventral sac. Arms unknown. Coal Measures; North America.

Erisocrinus, M. and W., and *Stemmatocrinus*, Trautsch., are without either *IRA* or radianal. The former has five minute infrabasals, which are covered by the stem; those of *Stemmatocrinus* are large and perfectly anchylosed so as to form a single plate. Certain Coal Measure species of *Erisocrinus* are scarcely distinguishable from *Encrinus liliiformis*. Sub-Carboniferous and Coal Measures; North America and Russia.

[*Encrinus*, Miller. The description of this genus is retained in its original position under the *Articulata*.]

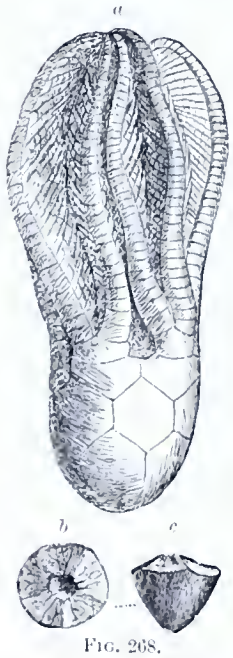


Fig. 268.

Agassizocrinus laevis, Roemer sp. Kaskaskia Group; Indiana. *a*, Crown, nat. size; *b*, Ventral aspect of the coalesced infrabasal disk; *c*, Side-view of same, nat. size (after M. and W.)

Fig. 269.

Scaphiocrinus multiplex, Trautsch. Upper part of Sub-Carboniferous; Moscow, Russia. Nat. size.

Family 10. **Agassizocrinidae.**
Wachsmuth and Springer.
(*Astylocrinidae*, Roemer.)

Base dicyclic. Dorsal cup elongate, with massive plates, and enclosing an extremely narrow visceral cavity. Infrabasals and basals very large; the former consisting of five elongate pieces, which form an almost solid semiovoid or semiglobose body. Radials very short, and proportionally smaller than the other plates of the cup. Anal and radianal both present. Structure of tegmen and ventral sac unknown. Arms ten. Sub-Carboniferous.

Agassizocrinus, Troost (*Astylocrinus*, Roemer), (Fig. 268). There is evidence that this form was fixed in its early stages by a stem, but subsequently became free-swimming. In the adult condition the scar where the column was attached, as well as the suture lines between the *IB*, became gradually obliterated by a secretion of calcareous matter over the whole surface of the plates. Restricted to the Kaskaskia Group of North America.

[Reference may be made here to Jaekel's recent Monograph, "Beiträge zur Kenntniss der palaeozoischen Crinoideen Deutschlands" (*Palaeont. Abhandl. von Dames und Kayser, neue Folge*, Bd. III.), 1895. Unfortunately this excellent memoir was not available before the present sheet was in print.—Trans.]

Order 4. FLEXIBILIA. Zittel.

(*Articulata*, p.p. W. and Sp.,[1] non Müller; *Ichthyocrinacea*, Neumayr.)

Base dicyclic, with stem or stemless; the proximal ring of the base in the latter case enclosing a (?) *dorsocentral* (Carpenter). *Arms branching, pinnulate or non-pinnulate. Tegmen, so far as has been observed, composed of orals and numerous exceedingly small, loosely united, movable pieces; orals asymmetrically arranged. Mouth and ambulacra exposed; the latter roofed over by covering pieces and enclosed by side-plates.* Ordovician to Carboniferous, and also Cretaceous.

Family 1. Ichthyocrinidae. Wachsmuth and Springer.

All plates of the calyx and of the arms from the radials upward united by loose suture or by muscular articulation. Base dicyclic; infrabasals three, unequal, small, rarely extending beyond the column, and fused with the top stem-joint; basals five, small. Radials succeeded by one to six costals, which in species without interradials increase in size upwards. Brachials united by more or less waving sutures, and their lower edges furnished with tooth-like projections which fit into depressions on the subjacent plates; occasionally the projections are developed as separate patelloid plates. Interbrachials, when present, rather irregularly arranged. Tegmen squamous; composed of five orals and numerous, very small, movable plates. Arms non-pinnulate, and exhibiting a very wide and shallow ventral groove. Column round; the upper ossicles extremely short, and generally wider than the others. Ordovician to Coal Measures.

Ichthyocrinus, Conrad (Fig. 270). *IB* very small; *R* and lower brachials laterally in contact at all sides; anals and interradials not represented. Crown appearing like a perfectly solid body when the arms are closed. Silurian to Coal Measures; North America and Europe.

Lecanocrinus, Hall (Fig. 271). Like the preceding, except that only four of the rays are laterally in contact, the two posterior ones being separated by a rhomboidal *RA* and a somewhat larger *IRA*. Silurian; North America and Europe.

Taxocrinus, Phill. (Figs. 272, 273). All five *R* separated by interbrachials. Costals two, sometimes three. The posterior *B* larger than the others, truncated, and supporting an *IRA*. This is followed by a longitudinal row of small elongate supplementary anals, which are interposed between numerous very minute irregular pieces. Plates of the four regular interrays less numerous, larger, and more symmetrically arranged. Ordovician to summit of Sub-Carboniferous; North America and Europe.

Gnorimocrinus, W. and Sp. Like *Taxocrinus*, but with *RA* in addition to *IRA*; the former also supporting a longitudinal row of supplementary anals. Silurian; Gottland.

Onychocrinus, Lyon and Cassed. Calyx depressed; arms spreading and talon-like. *IB* rarely projecting beyond the *R*, and closely or only partially

[1] [The three families embraced under this order, the *Ichthyocrinidae*, *Marsupitidae*, and *Uintacrinidae*, are included by Wachsmuth and Springer under the *Articulata* (*Articulosa*) as redefined by them. The non-pinnulate *Ichthyocrinidae*, however, are placed in a separate sub-order under the name of *Articulata Impinnata*; while the *Marsupitidae*, *Uintacrinidae*, and most of the Mesozoic and Recent Crinoids constitute the second sub-order *Articulata Pinnata*.—Trans.]

fused with the top stem-joint. The posterior *B* larger than the rest, and truncated or excavated at its upper face. Costals three to six, decreasing in size upwards; the two lower ones laterally united by a few large interbrachials. The posterior interray markedly different from the others; composed of a large number of exceedingly minute pieces, which enclose a longitudinal row of six to twelve moderately small, quadrangular, anal plates, supporting a small tube at the upper end. Tegmen formed by small, almost microscopic limestone particles, and extremely flexible. Arms ten, giving off clusters of armlets either from the sides at intervals, or only at their upper ends. Middle Sub-Carboniferous; North America and England.

Forbesiocrinus (de Kon. and le Hon), Hall. Differs from *Taxocrinus* in the construction of the anal area. *IRA* and *RA* both represented. Inter-

Fig. 270.

Ichthyocrinus laevis, Conrad. Perfect crown. Silurian (Niagara Group); Lockport, New York (after Hall).

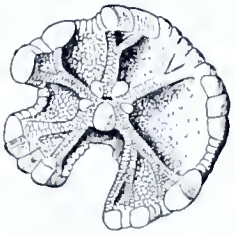


Fig. 272.

Taxocrinus intermedius, W. and Sp. (after Wachsmuth and Springer).

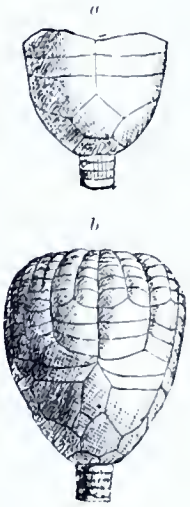


Fig. 271.

Lecanocrinus Billingsi, Ang. Silurian; Gottland. *a*, Calyx, seen from one side (right and left reversed); *b*, Crown, seen from the anal side (after Angelin).

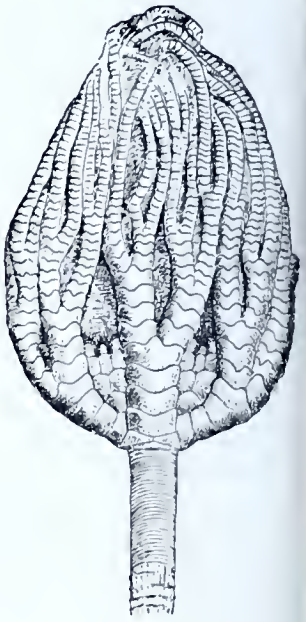


Fig. 273.

Taxocrinus Meeki, Hall sp. Perfect crown. Sub-Carboniferous; Crawfordsville, Ind.

brachials very numerous, arranged in some cases in twelve or more rows. Arms long, bifurcating, rather closely apposed, and with infolding tips. Sub-Carboniferous; North America and Europe.

Mespilocrinus, de Kon. and le Hon. Crown small and unsymmetrical, owing to the dextrorse arrangement of the arms. Posterior *B* truncated, and supporting a small *IRA*, which is the only supplementary plate of the dorsal cup. Costals and distichals two, followed by a very few free arm-plates. Arms very short, closely folded, and inclining to the right, owing to the cuneate form of lower brachials. Sub-Carboniferous; North America and Europe.

Homalocrinus, *Anisocrinus*, *Calpiocrinus*, *Cyrtidocrinus*, *Pycnosaccus*, Ang.; *Lithocrinus*, W. and Sp. Silurian, Gottland.

Family 2. **Marsupitidae.** d'Orbigny.

Base dicyclic. Dorsal cup large, composed of large, thin plates. Column absent; represented by a thin pentagonal, (?) dorsocentral, or centrodorsal plate.[1] *Infrabasals five; basals five; radials five; interradials and anals wanting. Upper edges of radials furnished with a small crescent-shaped articular facet, having a perforated transverse ridge. Arms branching, uniserial, and traversed by dorsal canals. Structure of tegmen and pinnules unknown.*

The only known genus is *Marsupites*, Mantell, occurring in the Upper Cretaceous (White Chalk) of England and Northern Germany (Fig. 274).

FIG. 274.

Marsupites testudinaris, Schlot. sp. Upper Cretaceous; Lüneburg, Prussia. *a*, Calyx, natural size; *b*, Radial, and a few of the arm-plates; *c*, Tips of the arms.

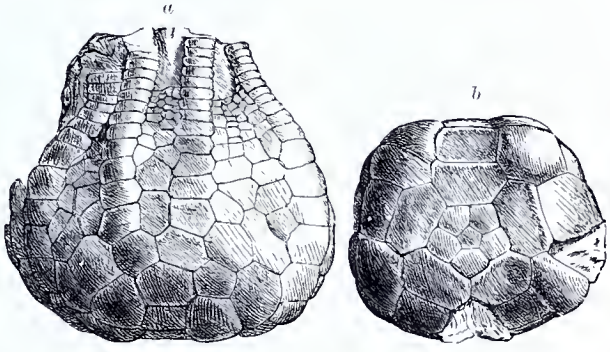


FIG. 275.

Uintacrinus Westphalicus, Schlüt. Upper Cretaceous; Recklingshausen, Westphalia. *a*, Calyx viewed from the side; *b*, Inferior aspect. Natural size (after Schlüter).

Family 3. **Uintacrinidae.** Zittel.

Symmetry perfectly pentamerous, plates thin, column wanting. Base monocyclic; basals five, enclosing a small, pentagonal, (?) dorsocentral, or centrodorsal plate. Costals two, the upper one axillary, and supporting two rows of distichals which are succeeded by palmars. Interbrachials numerous, the lowermost ring interposed between the costals. Arms long and pinnulate; composed of very short, almost circular ossicles. Pinnules heavy and closely abutting; the lower ones united by sutures, and incorporated into the calyx.

The solitary genus *Uintacrinus*, Grinnell (Fig. 275), occurs in the Upper Cretaceous of Kansas and Westphalia.

Order 5. ARTICULATA. Johannes Müller.

(*Neocrinoidea*, Carpenter; *Pentacrinacea*, Neumayr.)

Tegmen coriaceous, studded with minute calcareous particles, or covered with well-defined small plates of irregular arrangement. Mouth and food-grooves exposed; orals

[1] [This plate is supposed by Carpenter to represent the distal plate of the stem, and not the proximal one.—TRANS.]

present in nepionic, frequently also in the adult stages. Plates of the dorsal cup heavy; basals and radials united by close suture; radials and lower brachials by muscular articulation or by syzygy. Radials laterally in contact, except in Thanmatocrinus; but small irregular plates are frequently interposed between the costals and distichals. Anal plates represented only in the larval stages. Arms uniserial and pinnulate, the ossicles pierced by a dorsal canal. Trias to Recent.

The *Articulata* include all Recent, Tertiary, and Mesozoic Crinoids, with the exception of *Marsupites*, *Uintacrinus* [and *Encrinus*, according to Wachsmuth and Springer]. They are chiefly characterised by the exposed condition of the mouth and food-grooves, as well as by a canal which perforates the arms. This is known as the *dorsal* or *axial canal*, and contains a nerve-band and fibres of connective tissue. Starting from the dorsally situated chambered organ (Fig. 276), there are five canals which traverse the basals as far as the centre, where they divide into two branches which continue upward through the radials and brachials; and there is also in the radials a ring-canal which serves to connect the longitudinal canals with one another. In young individuals these canals are in the form of open grooves on the inner side of the plates, but they become perfectly closed in the adult condition.

Fig. 276.

Diagram showing course of axial canals in the calyx and arms of *Encrinus*. Canals represented by dotted lines when penetrating the interior of the plates, and by heavy lines when exposed on the inner side of the calyx (after Beyrich).

[To the *Articulata* (*Articulosa*) Wachsmuth and Springer refer only the *Pseudomonocyclica*; that is to say, Crinoids which are constructed on the dicyclic plan, but in which the infrabasals are rudimentary, and are more or less completely fused with the top stem-joint, and in which the last-named joint is not the youngest in the stem, as is the case in all other forms. The families thus embraced are the *Apiocrinidae*, *Bourgueticrinidae*, *Eugeniacrinidae*, and *Comatulidae* among Mesozoic and later Crinoids, and the *Ichthyocrinidae* among the Palaeozoic. The *Ichthyocrinidae*, which are devoid of pinnules, are placed in the sub-group *Articulata Impinnata*; the others, which are all pinnulate, constitute the sub-order *Articulata Pinnata*. The *Pentacrinidae* and *Encrinidae*, both of which are in all probability derived from the *Poteriocrinidae*, are assigned by these authors to the *Fistulata*, and the same is also true of the *Plicatocrinidae* and *Holopidae*, in which the top stem-joint is the youngest joint of the column wherever the latter is represented.]

Family 1. **Encrinidae**. Roemer.

Dorsal cup low, saucer-shaped, with dicyclic base. Infrabasals five, very small, and covered by the upper stem-joint. Basals five, large; radials five, the articular faces truncate, and provided with transverse ridges. Interbrachials absent, tegmen in the form of a vault. Arms 5×2 *or* 5×4; *heavy and simple, closely abutting, and either biserial or composed of alternately arranged cuneate joints. Column round, rarely giving off cirri; the terminal end thickened and laterally extended.* Trias.

Encrinus, Müller (Figs. 276-278). *R* succeeded by two costals, of which

the upper one is axillary, and supports the distichals. Union between the *R* and first costals and between the axillary costals and first distichals is by muscular articulation; the two costals and the two proximal distichals form

Fig. 277.

Encrinus liliiformis, Miller. Muschelkalk; Braunschweig.

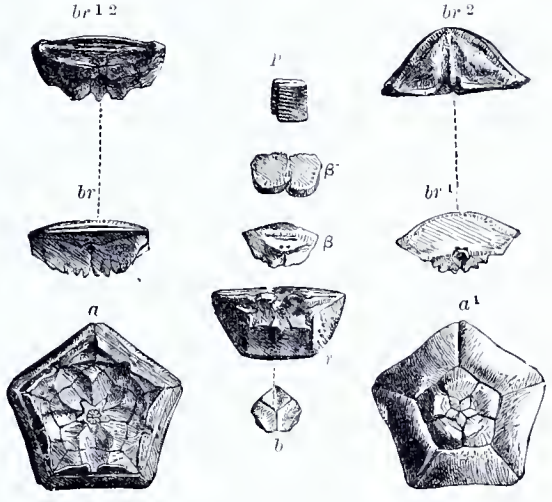


Fig. 278.

Portions of the calyx and arms of *Encrinus*. *a*, Interior of calyx; a^1, Exterior of same; *b*, Basal, upper surface; *r*, Radial, inner surface; β, One of the uniserial, and β*, biserial arm-plates; both of them traversed by duplicate dorsal canals; *p*, Pinnule ossicle (enlarged); *br*, First brachial, under surface; $br^{1\,2}$, First and second brachials joined together; inside, seen from below; br^1, First brachial, upper surface, showing line of syzygial suture; br^2, Second brachial (axillary), showing articular facets.

a syzygy, with their apposed faces dotted. Arms ten, or exceptionally twenty; uniserial at their lower ends, but rapidly becoming biserial. Upper and lower faces of stem-joints marked over their whole surface or only around their outer margins with radiating striae. Central canal small, round. Abundant in the Trias, especially in the German Muschelkalk. The stem-fragments of *E. liliiformis* not infrequently form massive beds of limestone (Trochitenkalk).

Dadocrinus, v. Meyer. Like the preceding, but smaller, and with uniserial arms. Trias.

Holocrinus, Jaekel. Trias.

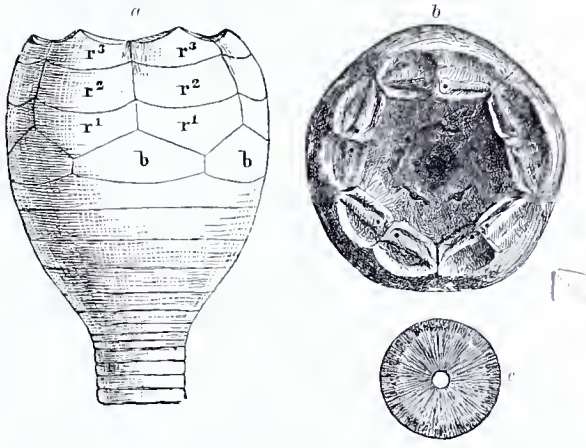


Fig. 279.

Apiocrinus Parkinsoni, Schlotheim. Great Oolite; Ranville, Calvados. *a*, Calyx and upper stem-joints, viewed from the side; *b*, Ventral aspect; *c*, Articular surface of one of the stem-joints (natural size).

Family 2. **Apiocrinidae.** d'Orbigny.

Calyx unsymmetrical, composed of heavy plates. Base pseudomonocyclic; the infrabasals completely fused with the centrodorsal, but rarely visible within the basal ring. Basals five, radials five, occasionally separated by a few interbrachials. Tegmen composed of

rather heavy plates; mouth and anus not observed. Arms uniserial, branching, and bearing long pinnules. Column round to sharply pentagonal, without lateral cirri; the proximal joint the largest of the stem; distal end thickened and forming a stout root. Jura, Cretaceous, and Recent.

Apiocrinus, Mill (Figs. 279-281). Dorsal cup pyriform, supported by a long cylindrical column, the proximal joints of which gradually expand in

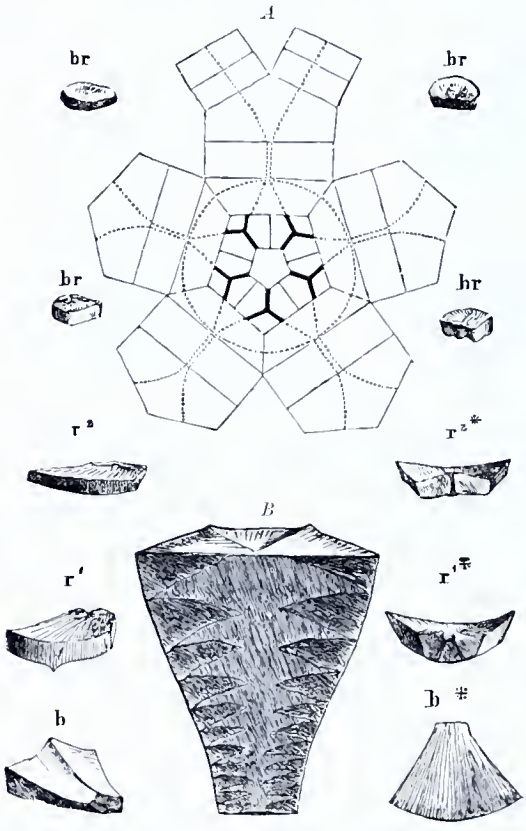


Fig. 280.

Fig. 281.

Fig. 280.

Apiocrinus Parkinsoni, Schloth. Great Oolite; Ranville, Calvados. *A*, Diagram of calyx, showing course of canals. These are represented by dotted lines when concealed within the plates, and by heavy lines where visible on the inner surface of the basals. *B*, Median longitudinal section through the uppermost stem-joints, showing empty space included between them; *b*, Basal, seen from above and from the inside; *b**, Lower surface of same; r^1, Radial, seen from without; r^{1*}, Inner aspect of same; r^2, and r^{2*}, Corresponding views of first brachial; *br*, Arm-plates. (Canals are invisible in plates above the basals, except where they have become exposed by weathering or abrasion.)

Fig. 281.

Apiocrinus Roissyanus, d'Orb. Upper Jura (Coral-Rag); Tonnerre, Yonne. Restoration (after d'Orbigny).

diameter, so as to become of equal width with the *B*. Upper face of the centrodorsal bearing five, low, angular ridges, which correspond in their disposition with the suture lines of the *IB*. Radials followed by two eostals, which are laterally and longitudinally united by rather close suture. Upper faces of the costals excavated and striated; the free brachials perforated, and furnished with well-defined transverse ridges. In a few species small interbrachials are interposed between the costals. Column round, the proximal joints in contact only near the periphery; inner portions of the joints wedge-shaped, and leaving a hollow space between them. Lias to Cretaceous.

Fragmentary stems occur notably in the Alps in great profusion, but calices are rare.

Guettardocrinus, d'Orb. Differs from the preceding in having costals immovably united with interbrachials. Solitary species: *G. dilatus*, d'Orb. Upper Jura.

Millericrinus, d'Orb. Closely allied to *Apiocrinus*, but articular facets of radials and brachials more strongly developed. Base occasionally with five minute *IB*, which are coalesced with the top stem-joint (centrodorsal); the latter extended laterally, and resting against the outer faces of the *B*. Column more or less sharply pentagonal, with the angles interradially directed. Lias to Lower Cretaceous.

Acrochordocrinus, Trautsch. Jura and Lower Cretaceous.

Calamocrinus, Ag. Recent; Galapagos Islands. (*Cf.* Literature, p. 124.)

Family 3. **Bourgueticrinidae.** de Loriol.

Dorsal cup small, pyriform, with shallow body-cavity, and composed of a centrodorsal, five basals, five radials, and one to two costals. Tegmen (in recent forms) coriaceous, and with mouth surrounded by five orals. Arms five, thin, uniserial, and bearing very long pinnules. Stem giving off numerous cirri; composed of heavy dice-box-shaped joints, both faces of which are provided with elevated transverse ridges, and deep ligamentous fossae. Jura to Recent.

Bourgueticrinus, d'Orb. (Fig. 282). Centrodorsal unusually large, as wide as the calyx at its greatest width, and wider than across the basals. *R*

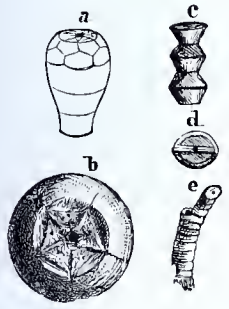


Fig. 282.

Bourgueticrinus ellipticus, Mill. White Chalk; Wiltshire. *a*, Calyx with centrodorsal and two of the stem-joints (nat. size); *b*, Ventral aspect (enlarged); *c*, Stem-joints; *d*, Articular surface of stem-joint; *e*, Cirrus.

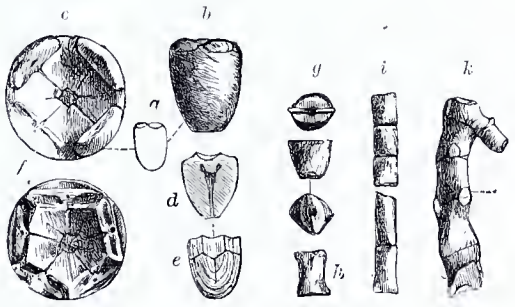


Fig. 283.

Rhizocrinus pyriformis, Goldf. sp. Eocene; Verona. *a*, *b*, Calyx from one side (nat. size and enlarged); *c*, Same from above, with three of the *Br* in place; *d*, Median longitudinal section of calyx (nat. size); *e*, Calyx with slightly abraded outer surface, showing suture lines between *B* and *R*; *f*, Calyx with five rays, seen from above (enlarged); *g*, *k*, Stem-joints (nat. size).

truncated at the upper face, and supporting very short costals. Structure of arms unknown. Column round; its joints almost as long as wide, the upper ones wider than the rest. Upper Jura to Tertiary.

Rhizocrinus, Sars. (*Conocrinus*, d'Orbigny non Troost), (Fig. 283). Base very large and elongate; composed of five heavy plates which are more or less fused. *R* typically five, but sometimes four, six, or seven; short and quadrate in form. Column slender, giving off branching cirri toward the distal end; composed of joints nearly three times longer than wide, and constricted in the middle. Eocene, and Recent at great depths.

Family 4. **Eugeniacrinidae.** Zittel.

(*Coadunata*, Miller; *Holopocrinidae*, pp. Jaekel.)

Dorsal cup composed of five (rarely four) thick, rigidly united radials resting upon a centrodorsal; basals invisible, tegmen unknown. Costals compressed, flange-like; united by syzygial sutures, or fused with one another. Arms uniserial, robust, and incurving. Stem short, destitute of cirri, and composed of but a few long cylindrical joints with granulated or striated articular faces. Dorsocentral thickened and expanded. Lias to Lower Cretaceous; Europe.

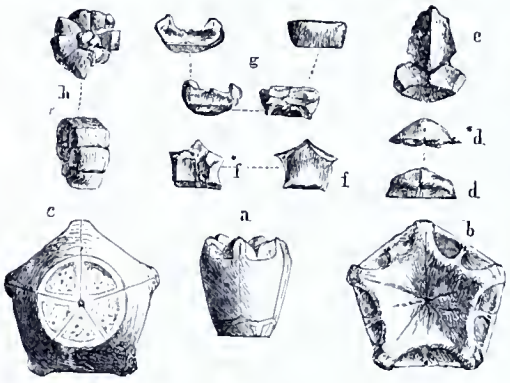


Fig. 284.

Eugeniacrinus caryophyllatus, Mill. Upper Jura; Streitberg, Franconia. *a*, Calyx with centrodorsal, seen from one side (nat. size); *b*, *c*, Ventral and dorsal aspects, $^3/_2$; *d*, *d**, First brachial, inner and upper surface; *e*, Second brachial, seen from the inside (nat. size); *f*, *h*, *E. nutans*, Goldf. Same locality; *f*, *f**, First and second *Br* fused together, seen from the outside and inside, respectively; *g*, Arm-plate, figured in four positions; *h*, Dorsal and lateral aspects of an inrolled arm.

Eugeniacrinus, Miller (Fig. 284). Dorsal cup small, saucer-shaped, and with shallow body-cavity. Centrodorsal covered with five radiating ridges. *B* invisible when the centrodorsal is attached, but from the course of the axial canals (Fig. 285) it is apparent that they are pushed upward so as to be completely enveloped by the *R*. The latter are very heavy, closely united, and sometimes completely anchylosed. The lateral margins of their upper faces are extended upwards so as to form conspicuous projections; the intermediate spaces are occupied by transverse ridges and deep fossae. Costals two, the upper one axillary. Structure of arms unknown. Abundant in the Upper Jura, notably in the Spongitenkalk of Southern Germany, Switzerland, France, and the Carpathians. Less common in the Dogger and Lower Cretaceous of the Alps.

Fig. 285.

Eugeniacrinus caryophyllatus, Mill. Upper Jura. *a*, Restoration, without the arms (after Fraas); *b*, Calyx broken open to show the silicified axial canals (after Jaekel).

Jaekel[1] divides *Eugeniacrinus* into the following subgenera:—*Cyrtocrinus*, *Sclerocrinus*, *Tetanocrinus*, *Eugeniacrinus*, s. str., and *Gymnocrinus*. The chief differential characters consist in modifications of the distichals, the arms, and articular surfaces of the radials.

Eudesicrinus, de Loriol. Stem reduced to two short thick segments which bear the five *R* directly. Lias.

Tetracrinus, Münst. *R* typically four, rarely three or five; apparently reposing directly upon the column, as no *B* or *IB* are visible. Upper face of the centrodorsal marked by four (sometimes three or five) prominent ridges which are radially disposed; lower face bearing about fifteen radiating prominences, which are

[1] Zeitschrift der deutsch. geol. Gesellsch. Bd. XLIII., 1891.

not continued over the median portion of the plate. *R* with transverse ridges and large muscular fossae. Stem-joints barrel-shaped. Jaekel regards the centrodorsal as representing the anchylosed *B*, notwithstanding the absence of axial canals. Upper Jura.

Phyllocrinus, d'Orb. Dorsal cup globose; upper edges of *R* with narrow articular facets, to either side of which are long, upright projections. Upper Jura and Lower Cretaceous, notably in the Mediterranean district.

Family 5. **Holopidae.** Zittel.

Base monocyclic; stemless. Dorsal cup beaker-shaped, and formed of five fused radials, by which the body was either directly attached, or, as was more probably the case, it was supported by a cycle of basals enclosed within the radials. Tegmen composed of five large triangular orals, surrounded by a narrow band of perisome. Arms 5 × 2, *uniserial, strongly incurving, and composed of large thick plates.*

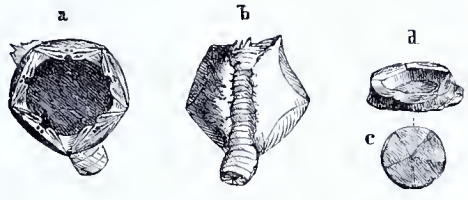


Fig. 286.

a, *b*, *Cotylederma docens*, Deslongch. Upper Lias; May, Calvados. *a*, Calyx seen from above; *b*, Same, from below; *c*, *d*, *C. lineata*, Quenst. Lias δ; Asselfingen; Baden. *c*, Centrodorsal; *d*, Circlet of fused basals. (All figures of the natural size).

Of the forms belonging to this family, *Cotylederma*, Quenst. (Fig. 286), is found in the Lias; *Cyathidium*, Steenstr. (*Micropocrinus*, Menegh.), in the Cretaceous and Tertiary; and *Holopus*, d'Orb., at great depths in existing seas.

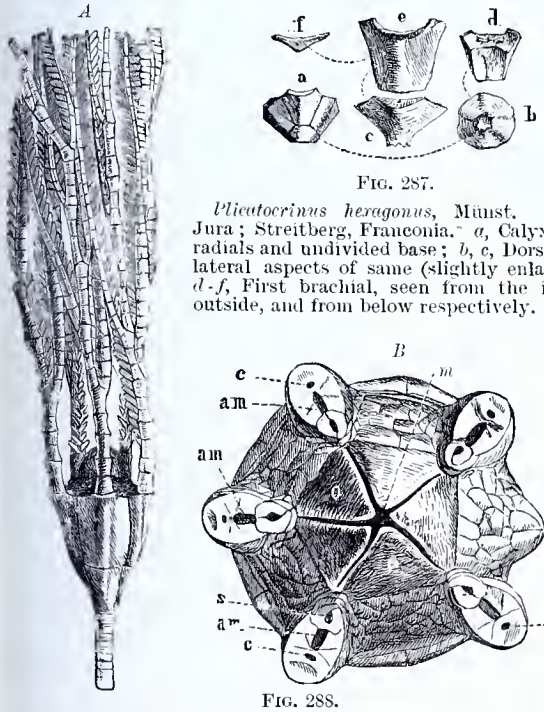


Fig. 287.

Plicatocrinus hexagonus, Münst. Upper Jura; Streitberg, Franconia. *a*, Calyx with radials and undivided base; *b*, *c*, Dorsal and lateral aspects of same (slightly enlarged); *d*-*f*, First brachial, seen from the inside, outside, and from below respectively.

Fig. 288.

Hyocrinus Bethellianus, Wyv. Thomson. Recent; Atlantic Ocean. *A*, Individual twice the natural size. *B*, Tegmen several times enlarged; *am*, Ambulacral furrows of the arms; *c*, Dorsal canals; *an*, Anus; *m*, Mouth; *o*, Orals (after Wyville Thomson).

Family 6. **Plicatocrinidae.** Zittel.

Base monocyclic, funnel-shaped, quadrangular to hexagonal, and formed of one solid piece. Radials four, six, or eight (rarely five or seven), short and delicate. These support axillaries, which give origin to two simple arms composed of wedge-shaped ossicles and united by muscular articulation. Pinnules usually composed of a single piece. Body-cavity wide and deep.

Plicatocrinus, Münst. (Fig. 287). Radials comparatively thin, their articular facets crescent-shaped; the outer faces longitudinally convex. Pinnules undivided, except the proximal ones, which consist of three pieces; they are angular or keel-shaped along the dorsal side, and deeply furrowed

on the ventral. Tegmen unknown. Upper Jura; a rare form, found in the Franconian and Swabian Alp.

Hyocrinus, Wyv. Thomson (Fig. 288). This recent form is obviously allied to the preceding, but differs from it rather conspicuously in the mode of branching of its arms. It has a heavily plated tegmen, with mouth surrounded by large orals. Carpenter regards it as the type of an independent family.

Family 7. **Saccocomidae.** d'Orbigny.

Calyx small, hemispherical, non-pedunculate. Radials five, very thin, elevated into prominent ridges along the median line, and enclosing an extremely small basal plate. Arms 5 × 2; *thin, widely separated, and giving off alternately towards the extremities simple incurving branches. Arm-plates cylindrical; each side of the ambulacral furrow lined with wing-like or spiniform projections. The entire skeleton exhibiting a reticulated structure with coarse meshes.* Upper Jura.

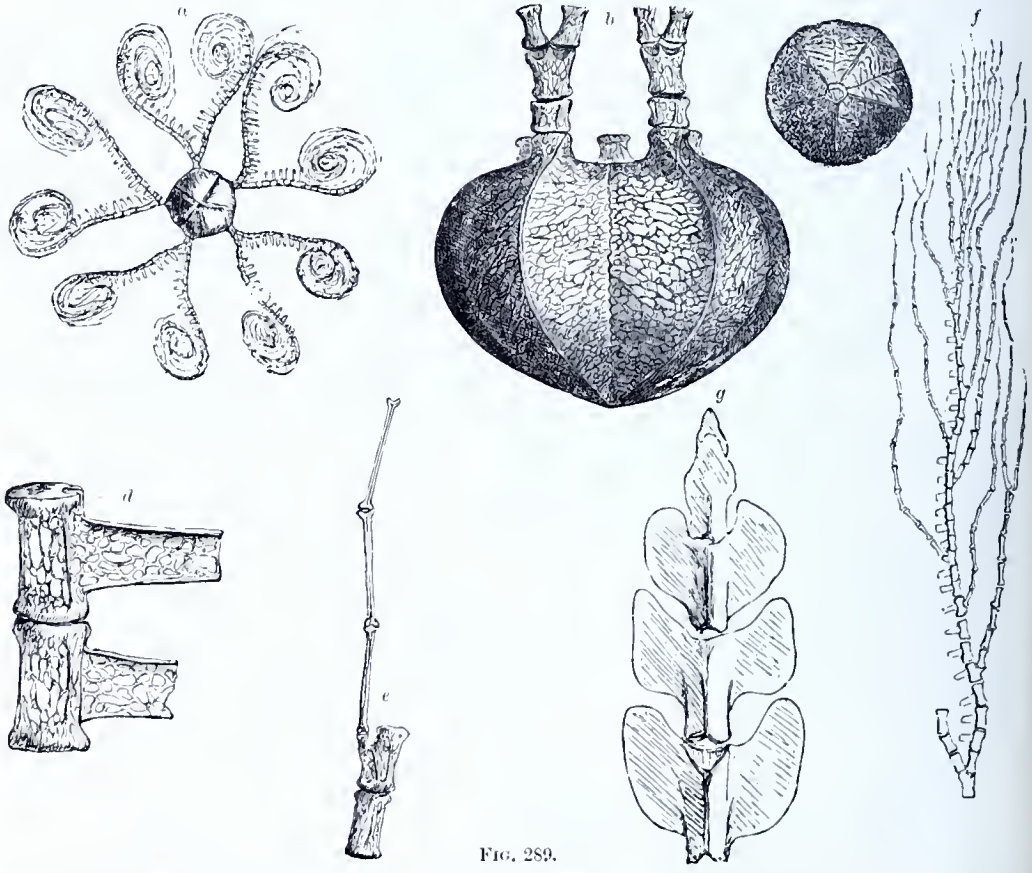


FIG. 289.

Saccocoma pectinata, Goldf. Upper Jura (Lithographic Slates); Eichstädt, Bavaria. *a*, Individual in natural size; *b*, Side view of calyx; *c*, Calyx seen from below, $^2/_1$; *d*, Two of the lower arm-plates; *e*, Two arm-plates of a higher order with one of the branches; *f*, The upper part of one of the arms straightened out; *g*, Lower brachials of *S. tenella*, Goldf. (Figs. *d* and *g* greatly, the others slightly enlarged.)

The only known genus, *Saccocoma*, Ag. (Fig. 289), occurs profusely in the Lithographic Slates of Eichstädt and Solenhofen, Bavaria. It is a free-swimming form, whose affinities with the monocyclic *Plicatocrinidae* were first clearly demonstrated by Jackel.[1]

[1] Zeitschrift der deutschen geol. Gesellsch. Bd. XLIV., 1892.

Family 8. **Pentacrinidae.** d'Orbigny.

Calyx small, bowl-shaped, and with dicyclic base; but the infrabasals are either rudimentary, or completely resorbed in the adult state. The top stem-joint always the youngest joint of the column. Basals five, radials five, costals one to two. Tegmen flexible, studded with small, irregular, calcareous particles or delicate plates. Arms strong, numerously branching, and pinnulate. Column long, pentangular or sub-pentagonal; its outer angles interradially directed; the cirri given off radially. Upper and lower faces of the stem-joints ornamented with a quinquelobate figure. Trias to Recent.

Pentacrinus, Miller (*Isocrinus*, v. Meyer; *Cladocrinus*, Ag.; *Cainocrinus*, Forbes), (Fig. 290). *IB* obsolete; costals rarely more than two, none of them pinnulate. Arms very numerously divided. Column more or less pentangular; the angles of the axial canal, contrary to the general rule in dicyclic forms, are radially directed, so as to correspond with the outer angles of the stem. Cirri very numerous; stem not thickened at its distal end. Trias to Recent; maximum in Lias.

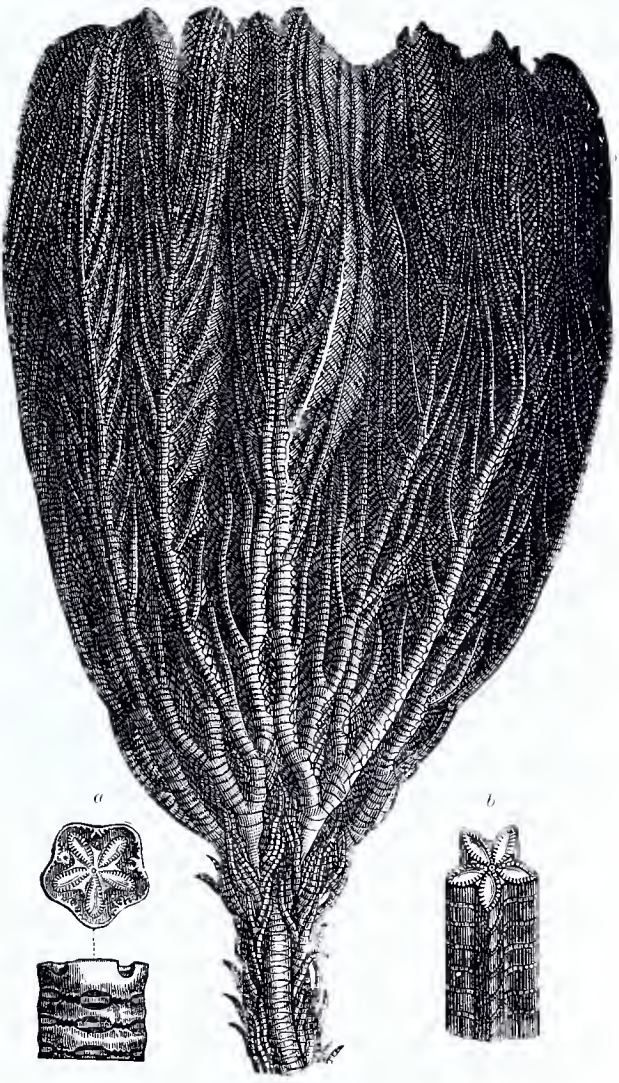


Fig. 290.

Pentacrinus (*Extracrinus*) *briareus*, Mill. Lower Lias; Lyme Regis, England (after Goldfuss). *a*, Stem-joints of *P. subangularis*, Mill. Upper Lias; *b*, Column of *P. basaltiformis*, Mill. Middle Lias.

Exquisitely preserved specimens are found in the Lower Lias of England, and the Upper Lias in the vicinity of Boll and Metzingen, Würtemberg. A slab containing no less than twenty-four perfect crowns of *P. subangularis*, Miller, with long intertwining stems, is preserved in the Tübingen Museum. There also may be seen a column which Quenstedt traced for over 70 feet, without reaching either end.

Metacrinus, Carp. Differs from *Pentacrinus* in that the *R* are succeeded by four to seven costals, of which the first and second form a syzygy. Where seven costals are present, the fourth and fifth are also united by syzygy. Angles of axial canal interradially disposed, so as to alternate with the outer

angles of the stem. Arms moderately branching. Cirri generally directed upwards; those of *Pentacrinus*, as a rule, downwards. Recent; Pacific Ocean.

Extracrinus, Austin. Base composed of five rudimentary *IB* and five *B*; radials with downward prolongations from their lower ends. The five interradial petals on the upper and lower faces of the stem-joints narrower and more lanceolate than in *Pentacrinus*. Lias to Recent.

(?) *Balanocrinus*, Ag. Stem-joints round, with serrated margins; articular faces marked by five crenulated ridges radiating from the centre. Lias to Cretaceous.

Family 9. **Comatulidae.** d'Orbigny.[1]

Pedunculate and fixed in nepionic stages, later losing the stem and leading a free existence. Base pseudomonocyclic; infrabasals visible only in the ciliated larva, afterwards becoming fused with the top stem-joint. Basals, which are large in the larval condition, are transformed at the end of the Pentacrinoid stage into the so-called rosette. Centrodorsal giving off numerous cirri after detachment of the stem; its angles interradially disposed, like the stem of dicyclic Crinoids. Tegmen coriaceous, naked or indurated by thin calcareous plates. Body-cavity very shallow; arms simple, interlocking, pinnulate. Lias to Recent.

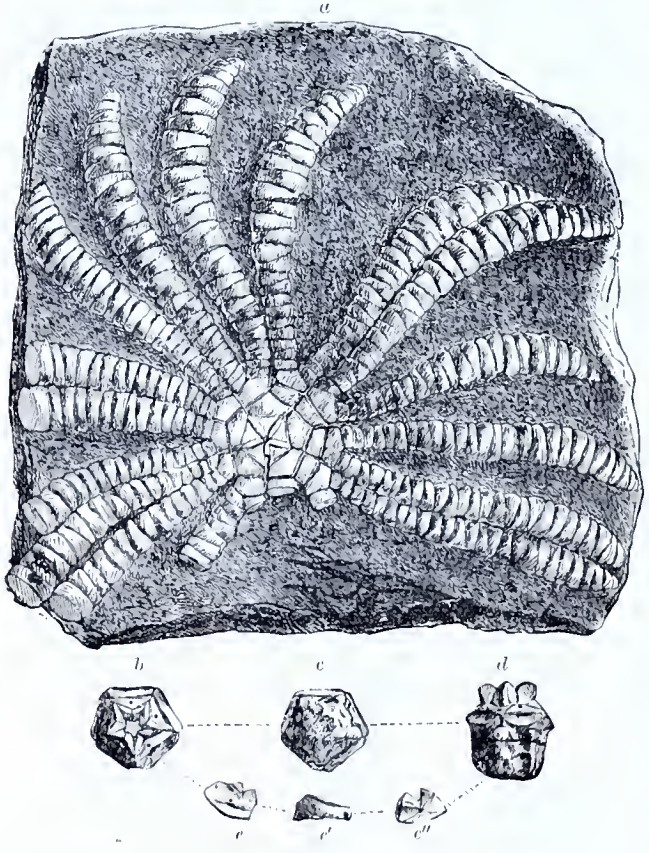


Fig. 291.

a, *Antedon* (*Solanocrinus*) *costatus*, Goldf. Upper Jura (Diceras-Kalk); Kelheim, Bavaria. Dorsal aspect of crown; centrodorsal and pinnules not preserved (slightly reduced); *b-d*, *A. scrobiculatus*, Goldf. Upper Jura; Streitberg, Franconia; *b*, Ventral; *c*, dorsal; and *d*, lateral aspect of calyx; *e*, Arm-plate.

Over 200 species are represented in the present seas, most of them being inhabitants of shallow water.

Antedon, Fréminv. (*Alecto*, Leach; *Comatula*, Lam.; *Pterocoma*, Ag.; *Decacnemos*, Bronn; *Comatulina*, d'Orb.; *Hertha*, Hagenow; *Solanocrinus*, *Glenotremites*, Goldf.), (Figs. 235, 291). Mouth central, anus eccentric; centrodorsal button-shaped. Costals two; the upper one axillary. Arms ten or more. Lias to Recent.

Eudiocrinus, Carp. (*Ophiocrinus*, Semper). Like *Antedon*, except that it has only five arms. Represented by one Neocomian and five Recent species.

[1] *Müller, J.*, Ueber die Gattung Comatula, etc. (Abhandl. Berlin. Akad.), 1847.
Ludwig, H., Beiträge zur Anatomie der Crinoideen (Zeitschr. für wiss. Zool. XXVIII.), 1877.
Carpenter, P. H., Report on the Crinoidea (Sci. Results, Chall. Exped., XI. and XXVI.), 1884-88.
Jaekel, O., Entwurf einer Morphogenie und Phylogenie der Crinoideen (Sitzber. naturf. Ges.), 1894.

Actinometra, Müller (*Comaster*, Goldf.; *Phanogenia*, Lovèn). Mouth eccentric or marginal; anus central or subcentral. Centrodorsal depressed, discoidal; covered with a single (rarely a double) row of cirri, or sometimes altogether naked. Jura to Recent.

Promachocrinus, Carp. Centrodorsal hemispherical or conical, and covered with numerous closely set cirri. *R* succeeded by a single costal; with high distal faces and large muscle plates. Mouth central; ambulacra symmetrically disposed. Recent.

Atelecrinus, Carp. Centrodorsal acorn-shaped, and bearing five double rows of cirri, those of each row alternating with one another and with those of adjacent rows. *R* separated from the centrodorsal by a complete circle of *B*. The first six or more orders of brachials devoid of pinnules. Recent.

Thaumatocrinus, Carp. Calyx plates as in the preceding, but with the addition of five large interradials resting upon the basals, followed by small irregular pieces between the costals at four of the sides; the posterior interradial bearing a short, solid, jointed appendage. Ventral surface covered by a narrow band of perisome, and almost entirely occupied by five large, symmetrically situated orals. Mouth central; anus eccentric, and extended in a short tube. Arms five. Recent; found at a depth of 1800 fathoms.

Range and Distribution of the Crinoidea.

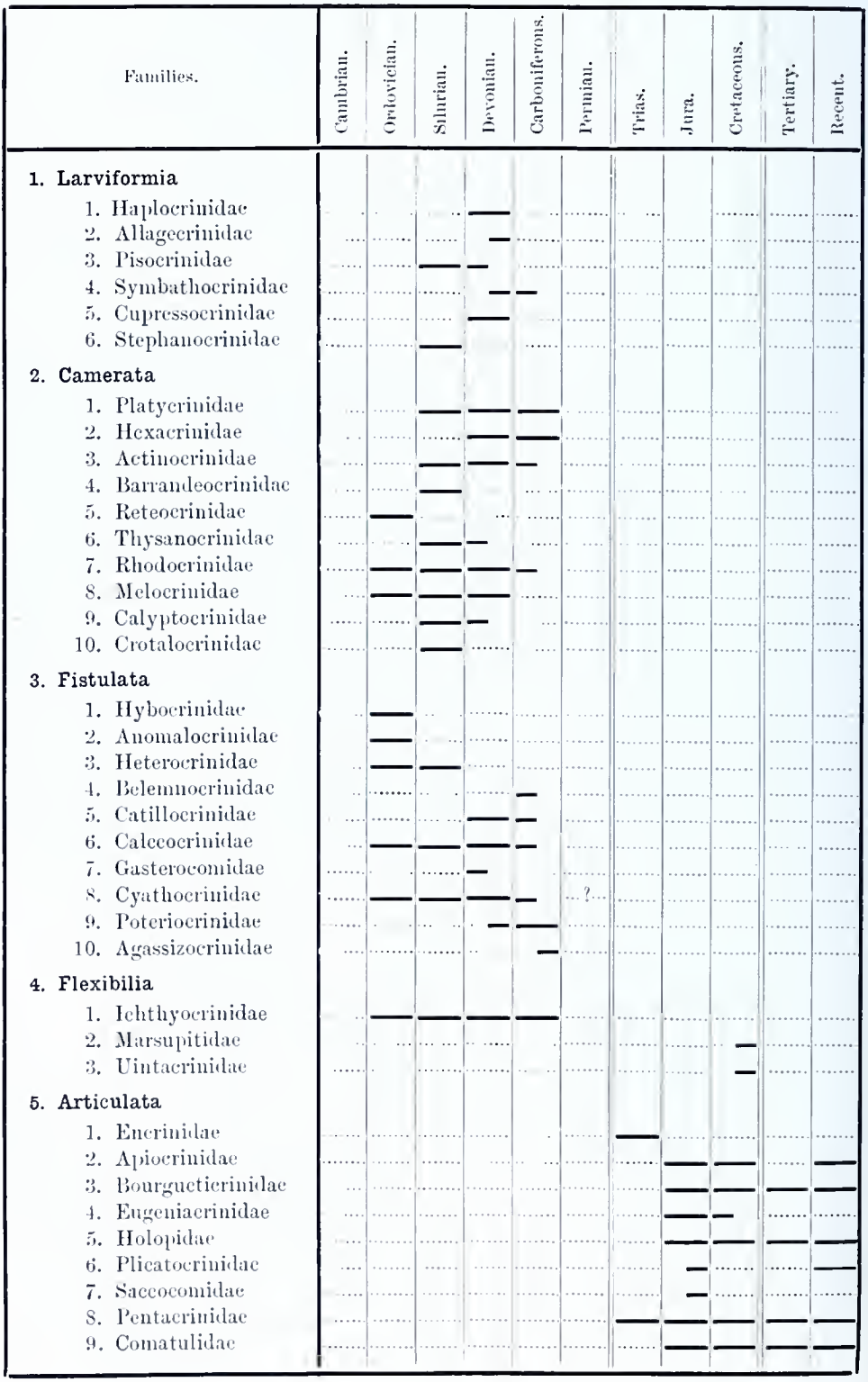
With the exception of the *Comatulidae*, all recent Crinoids (*Pentacrinus*, *Metacrinus*, *Rhizocrinus*, *Bathycrinus*, *Calamocrinus*, *Hyocrinus*, *Holopus*) are deep-sea inhabitants; and in many instances our knowledge of them is based upon but a few sporadic specimens. Of the *Comatulidae*, over 200 recent species have been described, the majority of which are found either in litoral zones, or in comparatively shallow water.

Crinoids attained their maximum development during the Palaeozoic era. The three principal orders—the *Larviformia*, *Camerata*, and *Fistulata*—are wholly confined to the Palaeozoic rocks; and with the exception of *Marsupites* and *Uintacrinus*, the same is also true of the *Flexibilia*. The *Articulata*, on the other hand, appear first in the Trias, and are represented continuously up to the present time. On this account Carpenter separated the Mesozoic and Cenozoic forms, under the term *Neocrinoidea*, from all earlier Crinoids, the latter being designated as *Palaeocrinoidea*. This distinction, however, has been shown to be largely artificial, and is now generally abandoned.

Crinoids, as a rule, have but a very local distribution; but in certain formations detached stem-joints and other fragments occur so profusely as to become of considerable rock-building importance; strata amounting to a number of metres in thickness are occasionally met with, which are almost wholly constituted of Crinoid remains.

While the great majority of recent forms are deep-sea inhabitants, the Palaeozoic, on the contrary, often characterise shallow water deposits, and are especially numerous in the vicinity of fossil coral reefs. Of the Mesozoic Crinoids, the *Eugeniacrinidae* and *Plicatocrinidae*, whose remains are commonly associated with those of Hexactinellid and Lithistid Sponges, probably lived at considerable depths; while, on the other hand, the *Encrinidae*, *Apiocrinidae*, *Saccocomidae*, and *Pentacrinidae*, were undoubtedly shallow water forms.

Table showing the Vertical Range of the Crinoidea.



Crinoidal fragments have been detected in the Cambrian, but consist of stem-joints only (*Dendrocrinus*). The Ordovician of England also yields a variety of stem-joints, and well-preserved calices of *Hybocrinus* and *Baerocrinus* occur in rocks of the same age in the vicinity of St. Petersburg. In North America, also, the Trenton and Hudson River limestones are locally very rich in Crinoid remains. The Silurian localities of Dudley and Wenlock, England, and especially the island of Gottland, Sweden, are famous for the surprising abundance and exquisite state of preservation of their fossil Crinoids. The Swedish forms alone comprise 43 genera and 176 species. The Silurian of North America, notably the Niagara Group, likewise contains a large variety of forms.

The best known Devonian localities are the Eifel, Rhineland, Nassau, Westphalia, the Ardennes, Asturias, Departement Mayenne, and North America. The Carboniferous Limestone of Tournay and Visé, Belgium, and that of England, Ireland, and the vicinity of Moscow, Russia, is occasionally charged with exceptionally well-preserved Crinoidal remains. But the most famous of all horizons is the Sub-Carboniferous Limestone of North America, where, in particular, the localities of Burlington, Iowa, and Crawfordsville, Indiana, have acquired a world-wide reputation.

The Permian has yielded but a single genus, which is doubtfully referable to *Cyathocrinus*. From the Trias only the *Encrinidae* and a few species of *Pentacrinus* are as yet known. The remaining members of the *Articulata* make their appearance in the Jura and Cretaceous, and with the exception of the *Saccocomidae*, are still represented in the existing fauna.

Class 2. CYSTOIDEA. Leopold von Buch.[1]

Extinct, pedunculate, or more rarely stemless Pelmatozoa, with calyx composed of more or less irregularly arranged plates. Arms imperfectly developed, sometimes absent. Calyx plates often finely perforate.

The calyx is globose, bursiform, ovate, or ellipsoidal in form, more rarely

[1] Literature:

Volborth, Alex. von, Ueber die Echinoencrinen (Bull. Acad. Imp. Sc. St. Petersb. vol. X.), 1842.
Volborth, Alex. von, Ueber die russischen Sphaeroniten (Verhandl. Mineralog. Gesellsch. St. Petersb.), 1845-46.
Buch, Leopold von, Ueber Cystideen (Abhandl. der Berliner Akad. für 1844), 1845. Translated in Quart. Journ. Geol. Soc. London, 1845.
Forbes, Edward, On the Cystidea of the Silurian Rocks of the British Islands (Mem. Geol. Survey Great Brit. vol. II., part 2), 1848.
Müller, Johannes, Ueber den Ban der Echinodermen (Abhandl. der Berliner Akad.), 1853.
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Billings, E., On the Cystidea of the Lower Silurian Rocks of Canada (Figures and Descriptions of Canadian Organic Remains, Decade III.), 1858.
Hall, James, Descriptions of some new Fossils from the Niagara Group (20th Ann. Rept. N.Y. State Cabinet of Nat. Hist.), 1867.
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Volborth, Alex. von, Ueber Achradocystites und Cystoblastus (Mém. Acad. Imp. Sci. St. Petersb., vol. XVI.), 1870.
Schmidt, Fr., Ueber Baltisch-Silurische Petrefacten (Mém. Acad. Imp. Sci. St. Petersb., vol. XXI.), 1874.
Barrande, Joachim, Système Silurien du Centre de la Bohême. Cystidées, vol. VII., 1887.
Carpenter, P. H., On Certain Points in the Morphology of the Cystidea (Journ. Linn. Soc. vol. XXIV.), 1891.

cylindrical or discoidal, and is composed of quadrangular, pentagonal, hexagonal, or polygonal plates, which are united by close suture. The plates vary in number from thirteen to several hundreds, and only exceptionally exhibit a regular arrangement. Sharp demarcations between the actinal and abactinal systems of plates, and between radial and interradial areas rarely exist; the plates of the sides of the calyx pass insensibly into those of the ventral surface, and are disposed in regular cycles only in a few instances. The base, however, is composed of a distinct ring of plates, and is usually recognisable by the presence of an articular surface for the attachment of a stem, or by being directly adherent to some foreign object.

The *mouth* is indicated by a central or subcentral aperture on the upper surface. It is sometimes covered by five small plates corresponding to the orals of Crinoids, and from it radiate from two to five simple or branching ambulacral grooves. The second opening on the ventral surface is situated eccentrically, and is frequently closed by a valvular pyramid, consisting usually of five or more triangular plates; or the covering may consist of a variable number of smaller pieces. This aperture, which was regarded by L. von Buch, Volborth, Forbes, and Hall as a genital opening, is now generally conceded to represent the *anus*. A third smaller opening, situated between the mouth and the anus, is present in a few forms only. The functions of this latter orifice are not well understood, but it is commonly regarded as the *ovarian aperture*, or *genital pore* (Fig. 292). Yet another small, slit-like opening, situated in the vicinity of the mouth, was detected by Barrande in the genus *Aristocystites;* but its functions are altogether unknown.

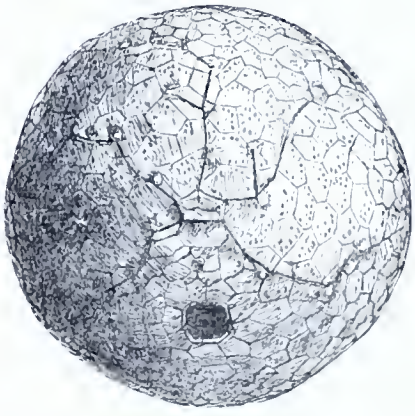

Fig. 292.

Glyptosphaerites Leuchtenbergi, Volborth. Calyx showing ambulacral grooves, plated mouth-opening, large laterally situated anus, and small ovarian aperture between mouth and anus.

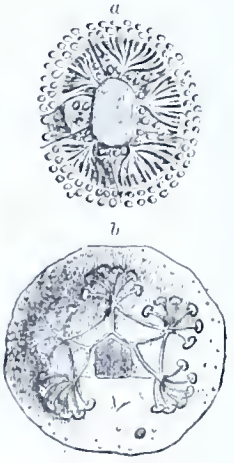

Fig. 293.

a, *Aristocystites*. Subtegminal ambulacral grooves; *b*, Same of *Pyrocystites*. Enlarged (after Barrande).

The *ambulacral grooves*, which are present in most Cystideans, are usually simple, although sometimes distally branching, and are frequently roofed over by alternately arranged covering pieces. In a few forms (*Caryocrinus*, *Cryptocrinus*, etc.) the grooves are wholly absent. The genera *Aristocystites*, *Pyrocystites*, and *Craterina* are without exposed ambulacral grooves; but they have instead, as Barrande discovered, a peculiar system of five or six covered passages on the inner surface of the calyx plates, which converge towards the mouth, and are distally more or less branching (Fig. 293). These structures, the so-called "*hydrophores palmées*," were homologised by Barrande with the hydrospires of Blastoids; but as Neumayr has pointed out, they are probably the equivalent of subtegminal food-grooves in Crinoids.

The calyx plates exhibit most remarkable structural peculiarities. As a

rule they are more or less extensively perforated by pores or fissures; although in some forms (*Cryptocrinus*, *Malocystites*, *Ateleocystites*, etc.) they appear to be imperforate, and are composed of a homogeneous calcareous layer of greater or lesser thickness, the same as in Crinoids. But in *Aristocystites*, *Craterina*, *Proteocystites*, *Glyptosphaerites*, *Echinosphaerites*, etc., the plates are uniformly covered both externally and internally with a very thin, generally smooth, calcareous membrane, which may be perforate or imperforate. The central layer is of variable thickness, and is traversed by numerous canals (Figs. 294, 295) which extend from the inner to the outer surface, sometimes rectilinearly (*Aristocystites*, *Craterinera*, etc.); sometimes in slightly sinuous lines; and in rare instances they divide dichotomously. The canals terminate on either surface in small round apertures or pores, which are arranged either singly or in pairs, and may or may not penetrate the outer calcareous membrane. The pores are commonly situated either on a tubercular elevation, or in a slight superficial depression.

FIG. 294.

Aristocystites. Canals perforating the median layer of plate.

But still more frequent than the canals are the so-called *pore-rhombs* (Fig. 296) which occur indifferently in types possessing numerous or but few calycine plates. The pores are arranged so as to form lozenge-shaped or rhombic figures, in such manner that one half of each rhomb belongs to one plate, and the other half to its contiguous neighbour; while the line of suture between the plates forms either the longer or the shorter diagonal of the rhomb. The pores of opposite sides of the rhomb are united by perfectly closed, straight ducts, which pass horizontally through the middle layer and across the line of suture between the two plates, thus producing a transversely striated appearance. Occasionally the connecting tubes appear on the outer surface as elevated striate rhombs; but as a rule they are concealed by the above-mentioned covering layer, and are only visible in weathered or abraded specimens. The pores of the rhombs also communicate with short canals passing vertically through the plates, the ends of which are either covered over by the outer calcareous layer, or appear on both surfaces as fine independent pores. A pair of oppositely situated pores of the latter description may sometimes receive as many as two or three fine canals, while in other genera they are entirely wanting.

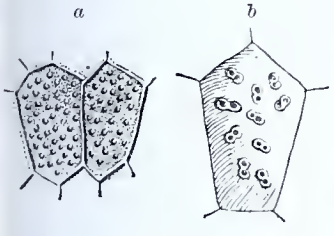

FIG. 295.

a, *Aristocystites*. Inner surface of two calyx plates showing simple pores; *b*, *Glyptosphaerites*. Outer surface of calyx plate showing double pores.

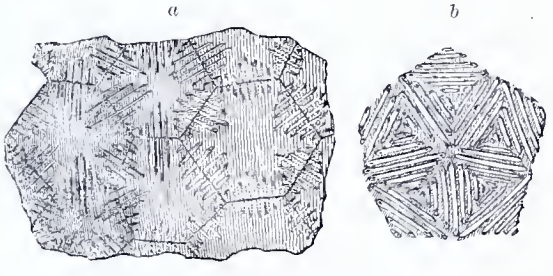

FIG. 296.

Pore-rhombs of (*a*) *Echinosphaerites*, and *b*, *Caryocrinus*, enlarged. The left half of Fig. *a* is abraded, so that the connecting tubes appear as open grooves.

The pore-rhombs are sometimes present upon nearly all plates of the calyx, but in other cases they are only developed on a certain number or on all of

the plates forming the side-walls of the calyx, being absent from its upper surface. In still other instances (*Pleurocystites*, *Callocystites*), (Fig. 297), the pore-rhombs are greatly reduced in number, and occur in the form known as "*pectinated rhombs*." The component halves of the latter stand on contiguous plates the same as the ordinary pore-rhombs, but are always separated externally by an interval; frequently the two parts are of different form or size, and sometimes one of them may become obsolescent.

As regards the functions of these canals and pores (the "hydrospires" of Billings), the anatomy of existing Crinoids furnishes us with no positive conclusions. They have been compared with the pores which are present in the tegmen of the latter, and the rather plausible suggestion has been offered that they served to admit water into the body-cavity, and thus performed respiratory functions. At all events, they could not have served for the protrusion of tube-feet, since they are frequently covered over by an outer calcareous membrane, which effectually shuts off communication with the exterior.

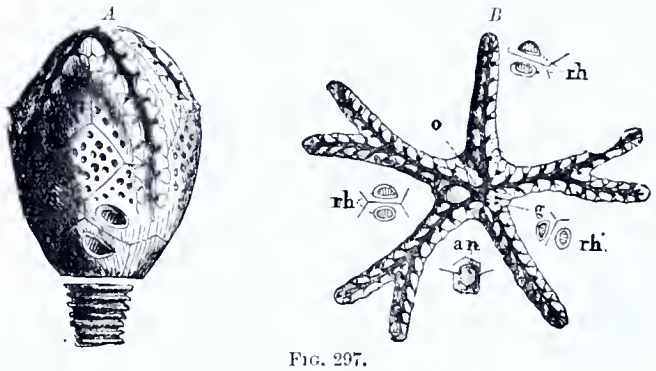

FIG. 297.

Callocystites Jewetti, Hall. Silurian (Niagara Group); Lockport, New York. *A*, Calyx from one side (natural size). *B*, Ambulacral grooves and three pectinated rhombs (*rh*), enlarged; *o*, Mouth; *an*, Anus; *g*, Genital pore (after Hall).

The *arms* in the Cystideans are but feebly developed, and are sometimes entirely (?) wanting, or they are but few in number (2, 3, 6, 9-13). The pentamerous symmetry, so generally characteristic of Echinoderms, pervades neither the arrangement of the calyx plates nor the number and disposition of the arms. The latter are invariably simple, are either uniserial or biserial, and exhibit a ventral groove protected by covering plates.

In some genera the arms attain considerable thickness, but in others they are very diminutive, and seem to have closer affinities with pinnulae than with the arms of Crinoids. In the *Callocystidae* and *Agelacrinidae*, as well as in the Canadian genera, *Amygdalocystites* and *Malocystites*, the arms either recline with their dorsal side facing the calyx, or they are incorporated into the calyx. The ventral side, in these cases, is directed outwardly, and the ambulacral furrow is bordered on either side by a row of alternating, jointed pinnules, which are attached by small articular facets running parallel with the groove. Pinnules have not as yet been observed in *Agelacrinus*, but the allied genera, *Mesites* and *Asteroblastus*, are furnished with delicate facets for their attachment.

The *stem*, as a rule, is greatly abbreviated, and is frequently obsolete. Sometimes the calyx is attached by the entire lower surface (*Agelacrinus*); or in other cases by means of a tubercular process (*Echinosphaerites*). Only in rare instances does the stem appear to have served for attachment, since it generally tapers distally to a point, and is invariably destitute of cirri. The stem sometimes resembles that of the Crinoids, in being composed of a number of short, prismatic, or cylindrical joints; these are pierced by a wide canal, and are either united by horizontal, striated, articular surfaces, or they over-

stride one another like the draw-tubes of a spy-glass. In other cases the upper part, and occasionally, indeed, the entire stem, is composed of vertical rows of alternating plates. These plates, as a rule (*Dendrocystites*), enclose a large central space, which may be regarded as a prolongation of the body-cavity.

The Cystideans constitute the oldest and least specialised group of the Pelmatozoa. Appearing first in the Cambrian, they develop a great variety of forms in the Ordovician and Silurian, but become extinct before the close of the Permian. While their own ancestry is obscure, it is highly probable that from them have descended both the Crinoids and Blastoids. If, on the one hand, the *Aristocystidae*, *Sphaerodontidae*, *Camarocystidae*, and *Echinosphaeritidae* differ radically from the Crinoids in respect to their numerously and irregularly plated calyx, or as regards the feeble development or even total absence of their arms; nevertheless, the *Cryptocrinidae* and the unfortunately ill-preserved Cambrian genus, *Lichenoides*, evince a striking similarity, especially as concerns the more or less regular arrangement of the calyx plates, and a certain approach to radiation. In fact, so far as the construction of the calyx alone is concerned, forms like *Porocrinus* and *Hypocrinus* may be assigned with equal propriety to either the Crinoids or Cystids. The presence of pectinated rhombs and calycine pores, however, and the porosity of the calyx plates, are characters which positively identify them as belonging to the latter class.

If we can account for the derivation of Crinoids from the Cystideans on the supposition that the calyx plates of the latter gradually took on a more definite arrangement, while the loss of pores and pore-rhombs was counterbalanced by a stronger development of the arms and the stem; so, too, it is possible to explain the origin of the Blastoids from the same source. Although hydrospires are clearly wanting in the Cystids, nevertheless, other characters, such as the recumbent attitude of the arms upon the sides of the calyx, or their insertion in grooves on the ventral surface, as well as an approach to ambulacral areas in certain forms (*Asteroblastus*), predicate an intimate relationship with the Blastoids. Probably the most notable similarities are presented by the peculiarly modified families, *Callocystidae* and *Agelacrinidae*. Various attempts have been made to affirm a connection between *Agelacrinus* and the *Asteroidea*, and between *Mesites* and certain of the primordial *Echinoidea* (*Cystocidaris*); but such hypotheses are scarcely warranted, since they proceed from an over-valuation of mere external resemblances, which are in nowise indicative of kinship.

The classification of the *Cystoidea* remains in a very unsatisfactory condition. This is owing in part to the comparative scarcity of material, as well as its frequently imperfect state of preservation; and in part to our insufficient understanding of many of the structural modifications. The classification of Johannes Müller was based primarily upon the structure of the calyx plates, and three main groups were recognised:—*Aporitidae*, *Diploporitidae*, and *Rhombifera*. These divisions, however, embrace a number of very heterogeneous elements, and in nowise fulfil the requirements of a natural system. The classifications proposed by Barrande and Steinmann are still more inadequate. It is advisable, therefore, to follow the example of Neumayr and Bernard, and merely arrange the different genera into families; the establishment of larger divisions being deferred until the group shall have been monographed.

Family 1. **Aristocystidae.** Neumayr.

Calyx composed of numerous heavy plates, arranged either irregularly or in successive zones, and covered on both sides by a calcareous integument. Calyx plates traversed by simple canals terminating on either surface in pores distributed either singly or in pairs. Ambulacral grooves subtegminal ("hydrophores palmées"); arms wanting; stem obsolete or very short. Ordovician.

Aristocystites, Barr. (Fig. 298). Calyx bursiform or ovate; ventral surface with four apertures. Ordovician (Etage D); Bohemia.

Deutocystites, Barr. Ventral surface with three apertures. *Craterina*, Barr. Conical, truncate. *Pyrocystites*, Barr. Clavate in form. All three genera in Ordovician (Etage D) of Bohemia.

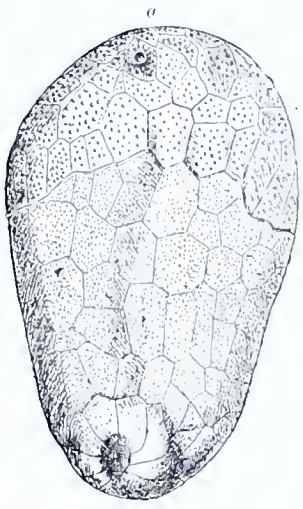

Fig. 298.

Aristocystites Bohemicus, Barr. Ordovician (*Dd* 4); Zahorzan, Bohemia. *a*, Side view; *b*, Summit aspect (after Barrande).

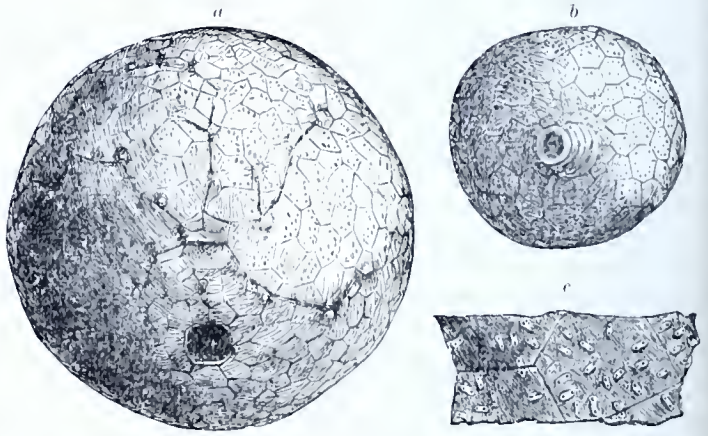

Fig. 299.

Glyptosphaerites Leuchtenbergi, Volborth. Ordovician; St. Petersburg. *a*, Calyx seen from above (natural size); *b*, Same from the dorsal face, with stem attached, reduced 1/2 (after Volborth); *c*, Calyx plates showing double pores (enlarged).

Fig. 300.

Protocrinites oviformis, Eichwald. Ordovician; Pulkowa, Russia. *a*, Calyx viewed from above; *b*, Same from below (after Volborth).

Family 2. **Sphaeronitidae.** Neumayr.

Calyx globular or cylindrical, short-stemmed or stemless, and composed of numerous irregularly arranged plates with pores united in pairs. Ambulacral grooves either open or protected by covering plates, and either short and simple, or elongated and branching. Arms as a rule exceedingly small and primitive. Ordovician and Silurian.

Sphaeronites, Hising. Globose, stemless. Five short ambulacral grooves

radiating from the mouth towards the arm bases. Ordovician (Vaginatenkalk); Russia, Sweden, and England. *S. pomum*, Gyll.

Glyptosphaerites, Müll. (Fig. 299). Differs from the preceding in having long, branching, ambulacral grooves, and a short, well-developed stem. Ordovician; Russia and Sweden.

Protocrinites, Eichw. (Fig. 300). Nearly hemispherical, non-pedunculate. Ambulacra grooves long and branching; arms unknown. Ordovician; Russia.

Fungocystites, Barrande. Clavate. Ordovician (Etage D); Bohemia.

Proteocystites, Barrande. Devonian (Etage F); Bohemia.

Holocystites, Hall (*Megacystites*, Hall). Elongated, cylindrical, or subcylindrical; short-stemmed or stemless; with subcentral mouth. Arms minute, springing from the ends of the ambulacral grooves. Silurian; North America, Gottland.

Eucystis, Angelin. Ordovician. *Gomphocystis*, Hall. Silurian.

Family 3. **Camarocystidae.** Barrande.

Calyx globose or discoid, composed of numerous polygonal plates, and sometimes fixed by the ventral surface. Interior of calyx divided into four to six compartments by partitions corresponding in position to lobes on the exterior. Stem long and slender. Silurian.

This family embraces two genera whose systematic position is still doubtful. The larger, *Camarocrinus*, Hall (= *Lobolithes*, Barrande), occurs in the middle and upper members of the Silurian in North America and Bohemia, and attains considerable size. The smaller, *Lichenocrinus*, Hall, is more or less crateriform, has a very long, tapering stem, and is invariably attached by its flattened ventral surface. It is found in the Ordovician (Hudson River Group) of North America.

Family 4. **Echinosphaeritidae.** Neumayr.

Calyx globular or bursiform, adherent or with short stem, and composed of numerous, irregularly arranged plates, all of which are furnished with pore-rhombs.

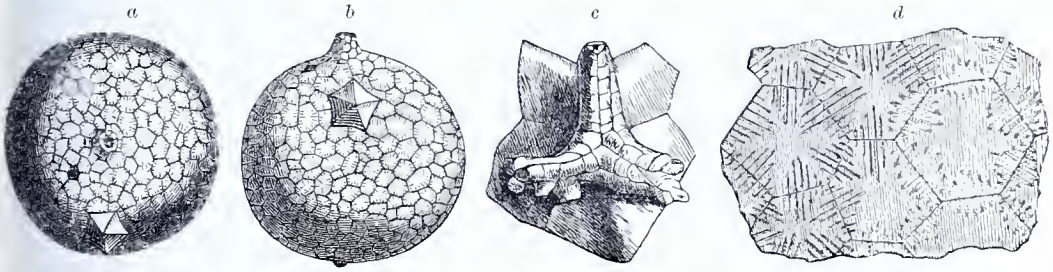

FIG. 301.

Echinosphaerites aurantium, Hising. sp. Ordovician (Vaginatenkalk); Pulkowa, Russia. *a*, Summit view of calyx; *b*, Calyx seen from the anal side; *c*, Mouth, arms, and covered ambulacral grooves; *d*, Calyx plates enlarged, showing pore-rhombs (cf. Fig. 296).

Ambulacral grooves short; arms two to five, free, biserial, rarely preserved. Stem, when present, composed of several vertical series of alternately arranged plates. Ordovician and Silurian.

Echinosphaerites, Wahlenb. (Fig. 301). Globose, non-pedunculate. Mouth central, ambulacral grooves short. Anal opening protected by valvular

pyramid; arms unknown. Very abundant in the Ordovician of Russia and Scandinavia. *E. aurantium*, Hising. sp.

Fig. 302.

Caryocystites granatum, Wahlb. sp. Ordovician; Oeland. Plates of the natural size showing elevated pore-rhombs.

Arachnocystites, Neumayr. Like the preceding, except that it has strong arms, usually three in number, which sometimes attain a length of 10 cm. Stem tapering distally to a point. Ordovician (Etage D); Bohemia. *A. infaustus*, Barr. sp.

Caryocystites, v. Buch (Fig. 302). Calyx plates relatively large. Pore-rhombs on external surface elevated, prominent. Stem wanting. Ordovician; Russia, Scandinavia, England. *C. granatum*, Wahlenb.

Orocystites, Barrande. Ordovician (Etage D); Bohemia.

Palaeocystites, Billings. Calyx ovate or pyriform; plates numerous, and poriferous at the margins. Ordovician; Canada.

Family 5. **Cryptocrinidae.** Zittel.

Calyx composed of three rings of very finely perforate or imperforate, somewhat regularly arranged plates. Mouth central, surrounded by articular facets for the attachment of small arms. Anus eccentric; stem round and slender. Ordovician to Permian.

Cryptocrinus, v. Buch (Fig. 303). Base composed of three plates, and surmounted by two zones, each containing five plates of unequal sizes. Mouth and anus enclosed within a ring of smaller pieces. Ordovician; St. Petersburg. *C. cerasus*, v. Buch.

Echinocystites, Hall. Ordovician; North America.

Porocrinus, Bill. (Fig. 304). Base composed of three plates, and succeeded by two circlets of regularly alternating pieces. Upper cycle giving rise to five feeble, uniserial arms. Small supplementary pieces furnished with pore-rhombs intercalated in the re-entrant angles between the calyx plates. Ordovician; Canada, Russia.

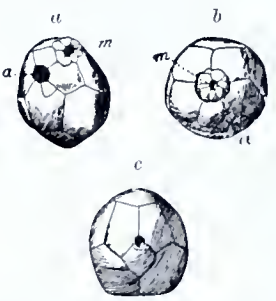

Fig. 303.

Cryptocrinus cerasus, v. Buch. Ordovician; Pulkowa, Russia. *a*, *b*, *c*, Calyx from one side, from above, and from below (nat. size); *m*, Mouth; *a*, Anus.

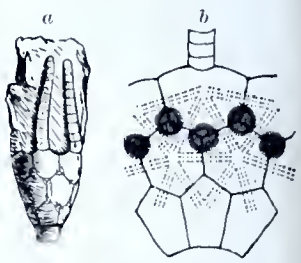

Fig. 304.

a, *Porocrinus conicus*, Billings. Ordovician; Ottawa, Canada. Nat. size (after Billings); *b*, *P. radiatus*, Beyr. Ordovician; St. Petersburg. Calyx plates showing pectinated rhombs. Considerably enlarged (after Beyrich).

Hypocrinus, Beyr. Base composed of three plates, and succeeded by two zones of alternately arranged, perforate plates. Mouth central. Permian; Timor.

Family 6. **Caryocrinidae.** Bernard.

Calyx composed of a moderate number of plates exhibiting a more or less definite arrangement in cycles. Certain or all of the side plates with pore-rhombs; those of the ventral surface imperforate. Arms three to thirteen, free, feeble. Stem constantly present, occasionally long. Ordovician and Silurian.

Hemicosmites, v. Buch. Calyx composed of four basal plates, two zones containing six and nine lateral plates respectively, and a circlet of six plates forming the ventral surface. The latter carries three short ambulacral grooves, at the ends of which are situated small articular facets for the attachment of arms. Rhomb-pores present on all of the side plates. Ordovician; Russia. *H. pyriformis*, v. Buch.

Caryocrinus, Say (Fig. 305). Calyx hexamerous, with dicyclic base. Infrabasals four, unequal; followed by a second row (basals) of six plates, alternating with the plates of the first and third cycles. The latter ring consists of eight plates, six of which, according to Carpenter, represent the radials, and two (the interscapulars of Hall) the interradials. Ventral surface formed of six or more small pieces. All plates of the cup furnished with pore-rhombs; the summit plates imperforate. Mouth and ambulacral grooves subtegminal. Anus protected by valvular pyramid, and situated on the outer margin of the ventral surface. Here also are placed the arms, which are six to thirteen in number, and relatively feeble. Stem long, composed of cylindrical segments. Silurian; North America (New York and Tennessee).

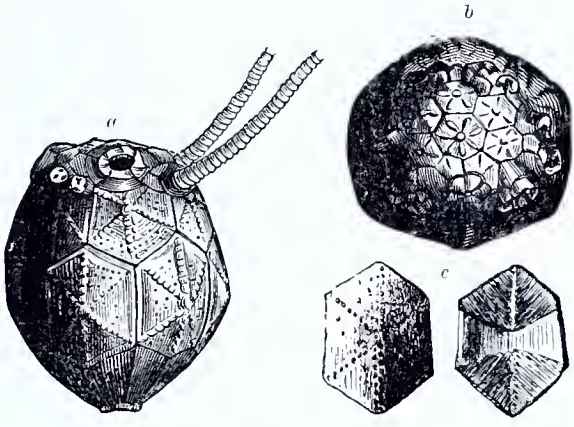

Fig. 305.

Caryocrinus ornatus, Say. Silurian; Lockport, New York. *a*, Calyx from one side, with two arms attached; *b*, Summit, natural size; *c*, Inner and outer surfaces of calyx plate of the second circlet, with pore-rhombs.

Fig. 306.

Echinoencrinus striatus, v. Buch. Ordovician; St. Petersburg.

Echinoencrinus, v. Meyer (*Sycocystites*, v. Buch), (Fig. 306). Calyx composed of four basal plates, and three cycles containing five plates each. All calycine plates ornamented with costae or ridges radiating outward from the centre. Ventral surface with short ambulacral grooves, and articular facets for the attachment of three small arms. Anus removed to a lateral position between the first and second circlet of side plates. Three pore-rhombs present; of these, two are situated above the base on the side opposite the anus, and the third above and slightly to the right of the anus. Stem round, short, tapering distally to a point, and composed of hollow segments inserted one within the other like the draws of a spy-glass. Ordovician; Russia.

Glyptocystites, Billings. Ordovician; Canada and Russia.

Homocystites, *Mimocystites*, Barrande. Ordovician; Bohemia.

Family 7. **Anomalocystidae**. Woodward.

Calyx more or less compressed, frequently with dissimilarly plated anterior and posterior sides. Plates either imperforate or with simple pores; pore-rhombs absent or but few in number. Arms free; stem short, tapering distally to a point. Cambrian to Silurian.

Trochocystites, Barr. Calyx strongly compressed. Plates of the right and left sides large, those of both the anterior and posterior small, polygonal. All plates perforate, but without pore-rhombs. Ventral surface with three apertures. Stem composed of several vertical rows of plates. Cambrian; Bohemia, Spain, Northern France.

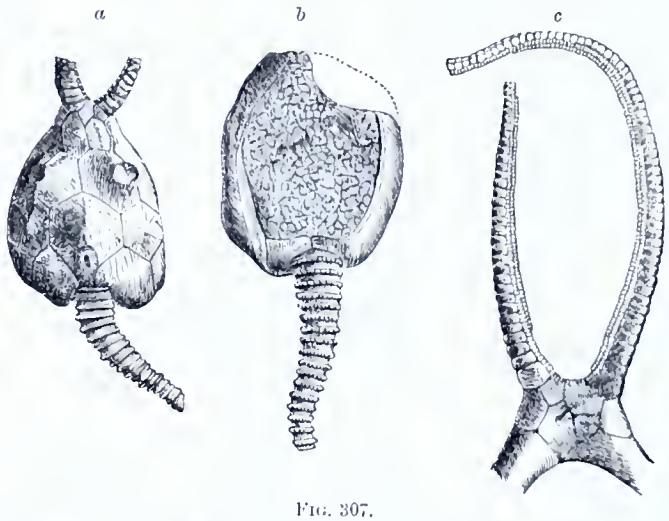

Fig. 307.

Pleurocystites squamosus, Billings. Ordovician; Ottawa, Canada. *a*, Calyx from the anterior side; *b*, Same from the anal side; *c*, Arms, enlarged. Right and left reversed (after Billings).

Mitrocystites, Barr. Like the preceding, except that one side of the calyx is composed of tolerably large, and the other of small plates. Ordovician; Bohemia.

Anomalocystites, Hall (*Aeteleocystites*, Bill.) Calycine plates smaller and more numerous on the convex side than on the concave. Anus situated very low down on the convex side. Arms feeble, filiform. Ordovician and Silurian; North America, England, Bohemia.

Balanocystites, *Dendrocystites*, Barr. Ordovician; Bohemia.

Pleurocystites, Bill (Fig. 307). Convex side with large plates arranged in cycles; flattened side covered with very minute plates. Three isolated pore-rhombs borne on the convex side. Arms two in number, robust. Stem round, tapering distally to a point. Ordovician; Canada.

Fig. 308.

Pseudocrinites quadrifasciatus, Pearce. Silurian; Tividale, England. *A*, Calyx from one side. *B*, Summit, showing mouth (*m*), anus (*a*), and three of the arms. The fourth arm (*a*) broken away, exposing flattened surface of calyx.

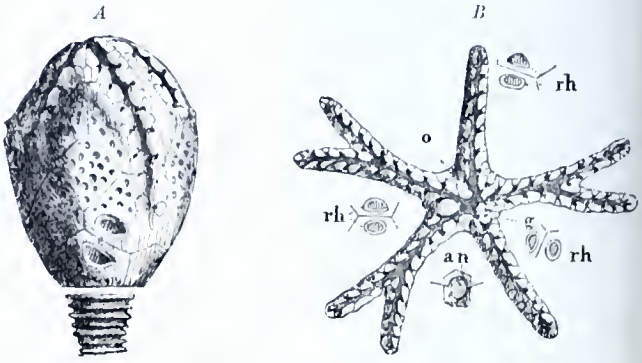

Fig. 309.

Callocystites Jewetti, Hall. Silurian (Niagara Group); Lockport, New York. *A*, Calyx from one side (natural size). *B*, Ambulacral grooves and three pectinated rhombs (*rh*), enlarged; *o*, Mouth; *an*, Anus; *g*, Genital pore (after Hall).

Family 8. **Callocystidae.** Bernard.

Calyx composed of large plates arranged in three or four cycles, and exhibiting three to five pectinated rhombs, the component halves of which stand on contiguous plates,

and are separated by an interval. Mouth slit-like, and forming the centre of radiation for two to five pinnulate arms which are protected by covering pieces, and either repose upon the calyx, or are sunk below the surface in grooves. Stem well developed, tapering distally to a point. Ordovician and Silurian.

Pseudocrinites, Pearce (Fig. 308). Calyx ovate, two- to four-sided, and composed of four cycles of polygonal plates. Anus closed by valvular pyramid, and occupying a lateral position. Pore-rhombs three in number; one placed above the base, the remaining two to the right and left of the anus. Arms two to four, recumbent upon the calyx, extending to the base, and beset with biserial jointed pinnules. Stem robust. Silurian; England.

Lepadocrinus, Hall; *Apiocystites*, Forbes. Silurian.

Callocystites, Hall (Fig. 309). Calyx with four pore-rhombs. Arms sometimes bifurcating. Silurian; North America.

? *Hybocystites*, Wetherby. Ordovician.

Family 9. **Agelacrinidae.** Hall.

Calyx composed of a large number of small, irregularly arranged plates, and either furnished with a short stem, or fixed by a broad base. Plates pierced by pores, usually united in pairs. Mouth central; anus eccentric, provided with valvular pyramid. Arms placed in radial grooves on exterior of the calyx, and protected by covering plates. Ordovician to Carboniferous.

Agelacrinus, Vanuxem (Fig. 310). Calyx in the form of a depressed or convex disk, stemless, and attached by the entire under surface; composed of numerous, small, polygonal, usually imbricating plates, which are perforated

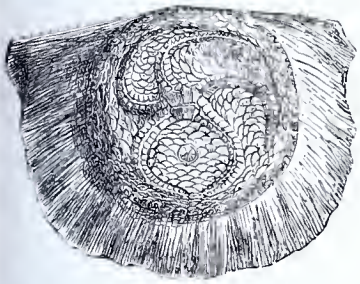

Fig. 310.

Agelacrinus Cincinnatiensis, Roemer. Ordovician; Cincinnati, Ohio. Individual of the natural size adherent to shell of *Strophomena alternata*.

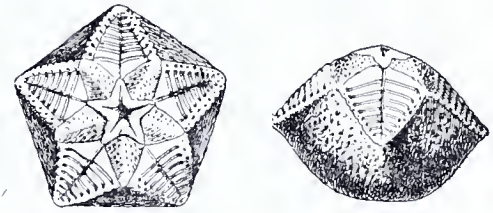

Fig. 311.

Asteroblastus stellatus, Eichwald. Ordovician; Pulkowa, Russia. Natural size (after Schmidt).

by fine, and, for the most part, conjugate pores. Mouth surrounded by four oral plates; radiating from this are five small, more or less curved arms, which are embedded in grooves on the outer surface, and are protected by a double row of covering plates. Ordovician; North America and Bohemia. Rare in Silurian, Devonian, and Carboniferous.

Sub-genera:—*Lepidodiscus*, *Hemicystites*, *Cytaster*, Hall; *Edrioaster*, Billings. Ordovician; North America.

Mesites, Hoffmann. Globose, with truncate base, probably pedunculate. Calyx plates small, polygonal, and exhibiting conjugate pores. Arms five, very small, embedded in radial grooves, and protected by covering plates; the latter are furnished with articular facets for the attachment of pinnules, and

are separated by small furrows conducting into the ambulacral grooves. Anus closed by a valvular pyramid. Ordovician; Russia, Bohemia.

Asteroblastus, Eichw. (Fig. 311). Calyx gemmiform, pentagonal, pedunculate, and composed of innumerable rigidly united plates which are perforated by conjugate pores. Upper surface marked by five large petaloid or stellate areas, which are covered with alternating plates, and correspond to the recumbent arms of *Agelacrinus*. Ordovician; Russia.

Tiaracrinus, Schlüt. (*Staurosoma*, Barr.) Devonian; Eifel, Bohemia.

Range and Distribution of the Cystoidea.

Not only are the Cystideans wholly extinct, but they also constitute the oldest known group of the *Pelmatozoa*. They are represented in the Cambrian by a number of poorly preserved forms, whose affinities are in many cases doubtful (*Protocystites*, *Macrocystella*, *Eocystites*, *Lichenoides*, *Trochocystites*). They attain the climax of their development in the Ordovician and Silurian, whereupon they suddenly diminish in numbers, and with the close of the Carboniferous they entirely disappear. Of the 250 species that have been described, scarcely a dozen are found in strata above the Silurian.

Although a few forms (*Echinosphaerites*, *Aristocystites*, *Caryocystites*) appear in considerable abundance in certain formations, and occasionally fill up whole beds, the majority are of comparatively rare occurrence. The arms and pinnules are only exceptionally preserved, owing to their fragile constitution; and the stem is also usually lost.

Cystideans are found most plentifully in the Ordovician rocks of St. Petersburg, Russia, and in the Silurian localities of Oeland, Gottland, Sweden, Wales, and Bohemia (Etage D). The Bohemian specimens are usually preserved in the form of casts and moulds, and are contained in silicious or argillaceous slates. The Chazy and Trenton limestones of Canada, New York, Ohio, and Indiana also yield a large variety of forms.

Excellently preserved specimens of *Pseudocrinites*, *Apiocystites*, *Echinoencrinus*, and *Anomalocystites* are obtained from the Silurian limestones of Dudley and Tividale, England; similar, and in part vicarious forms (*Lepadocrinus*, *Callocystites*, *Caryocrinus*) being found in the Silurian (Niagara Group) of North America. Only scanty remains are known from the Devonian (*Proteocystites*, *Anomalocystites*, *Agelacrinus*, and *Tiaracrinus*); and but two genera (*Agelacrinus* and *Lepadocrinus*) are represented in the Lower Carboniferous. The last surviving genus is *Hypocrinus*, which is confined to the Permo-Carboniferous of Timor.

Class 3. BLASTOIDEA. Say.[1]

Extinct, short-stemmed, or stemless Pelmatozoa with a large rigid calyx, which resembles a flower-bud in shape, and is generally composed of thirteen principal

[1] *Say, Thomas*, Observations on some Species of Zoophytes, etc. (Am. Journ. Sci. vol. II.), 1820.
Say, Thomas, On two Genera and several Species of Crinoids (Journ. Acad. Nat. Sci. Philad. vol. IV. p. 289), 1825. (Also in Zool. Journ. vol. II. p. 311), 1825.
Roemer, Ferdinand, Monographie der fossilen Crinoideenfamilie der Blastoideen (Troschel's Archiv. für Naturgeschichte, Bd. XVII. pp. 326-397), 1852.
Rofe, John, Notes on Echinodermata (Geol. Mag., Dec. 1, vol. II.), 1865.

plates; with recumbent ambulacra, which support at their lateral margins numerous pinnule-like appendages, and are provided along their inner floor with lamellar tubes known as hydrospires.

The *calyx* is clavate, pyriform, ovate, or globose, frequently pentangular at its upper face, and composed of plates which are firmly united among themselves. The plates of the abactinal system are arranged in three successive cycles, represented by the basals, radials, and interradials. The plates of the actinal system comprise the summit plates and the ambulacra.

The *basals* consist of two plates of equal size, and a third smaller one, which is directed invariably toward the right anterior interradius. Resting upon the basals are five V-shaped, usually equal *radials* (commonly known as "*forked plates*"), whose superior margins are more or less deeply incised by the *radial sinuses*. The term sinus is applied to the open space between the two prongs or *limbs* of the plate.

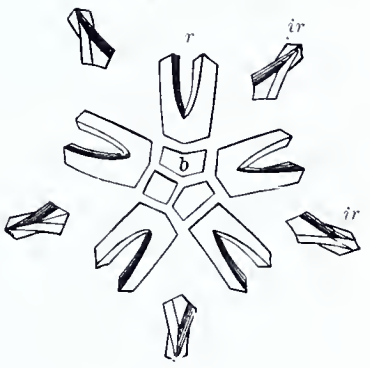

FIG. 312.

Pentremites Godoni, Defr. sp. Diagram of calyx. *b*, Basals; *r*, Radials; *ir*, Interradials or deltoids.

Succeeding and alternating with the radials, and resting upon their limbs, are five *interradial* or *deltoid plates*, which vary excessively in size. In some species they occupy a large part of the sides of the calyx, and in others they are confined to the upper face. In *Elaeacrinus* and certain species of *Granatocrinus*, the deltoids extend down so far into the calyx as to constitute more than half, or nearly the whole of its sides, while the radials are so short as to be almost invisible in a side view. Most writers refer the deltoids to the plates of the tegmen, but they properly form a part of the dorsal cup. Only a part of the deltoids is exposed to view, their sides being provided with flanges which are covered by the proximal ends of the ambulacra. The name deltoid has reference to the exposed part of the plates, which in most forms is triangular or rhomboidal in outline.

The radial sinuses between the limbs of the radials and the superjacent deltoids are filled by the *ambulacral fields* or *ambulacra* ("*pseudoambulacra*" of Roemer). The ambulacra vary in form from petaloid to narrow lanceolate or linear, and extend from the summit of the calyx to the distal ends or *lips* of the radial sinuses. The open space in which the ambulacra meet, the so-called "*summit-opening*," is pentangular, and central in position. Ordinarily this space is unobstructed, but in well-preserved specimens it is covered by a greater or lesser number of minute calcareous pieces (Fig. 313); these may be either regularly or irregularly arranged, but leave at each angle of the summit-opening a small passage-way, by means of which the ambulacra communicate with the peristome. The mouth is invariably subtegminal.

[The summit structure is rarely observed. The covering in *Elaeacrinus* consists of five asymmetrical orals; similar orals, surrounded by smaller plates, are present in *Orophocrinus*, and in *Schizoblastus Sayi;* but in *Granatocrinus*

Billings, E., Notes on the Structure of Crinoidea, Cystidea, and Blastoidea (Am. Journ. Sci. 2nd. ser. vols. XLVIII., XLIX., and L.), 1869-70.

Etheridge, R., and *Carpenter, P. H.*, Catalogue of the Blastoidea in the Geological Department of the British Museum, 1886. [Complete bibliography, pp. 303-310.]

Norwoodi and in *Cryptocrinus melo*, the summit is paved by numerous, very minute, irregularly arranged pieces. In the genus *Pentremites*, as observed in five or six species, the summit is surmounted by a pyramid formed of five elongate, tapering spines, the outermost of which are shorter than the rest. This pyramid not only conceals the summit-opening, but also extends over the greater part of the spiracles and the anal aperture; but it leaves at

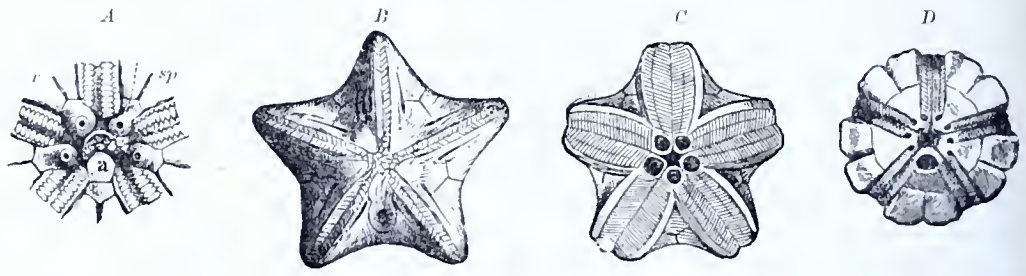

Fig. 313.

A, *Granatocrinus Norwoodi*, O. and S. Upper face of perfect specimen, with mouth and anus (*a*) closed by plates. Spiracles (*sp*) separate. *B*, *Orophocrinus stelliformis*, O. and S. Upper face with closed peristome and exposed anus. Spiracles slit-like. *C*, *Pentremites sulcatus*, Roem. Central mouth-opening surrounded by five spiracles, the posterior one confluent with the anus. *D*, *Cryptoblastus melo*, O. and S. sp. Upper face with central mouth-opening, large anus, and eight spiracles (after Carpenter).

the median line of each ambulacrum a channel communicating with the peristome.]

The summit in most Blastoids is surrounded by a cycle of five pairs of openings; and between the two posterior ones there is usually interposed a single additional aperture. The former were regarded by Roemer as connected with the genital system, and were called by him "*ovarian apertures*"; but they are now known as the *spiracles*. The other opening which pierces the upper end of the posterior deltoid is the *anus*.

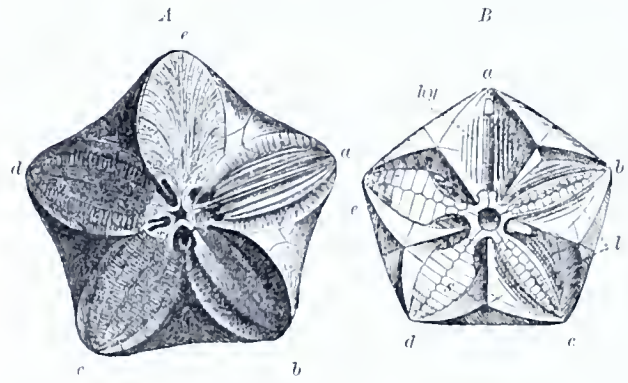

Fig. 314.

A, *Pentremites Godoni*, Defr. sp. Upper face with ambulacral fields in various states of preservation. *a*, Ambulacrum after the removal of lancet- and side-plates; hydrospires exposed; *b*, Lancet-plate with upper surface denuded by weathering; *c*, Perfectly preserved lancet-plate bordered by side-plates; *d*, The same, but with transverse markings of lancet-plate obliterated; *e*, Ambulacrum covered with pinnules (after Roemer). *B*, *Phaenoschisma acutum*, Sow. sp. Upper face, enlarged; *a*, Ambulacrum after removal of the lancet- and side-plates; hydrospire slits (*hy*) cutting through radials and deltoids; *b*, *c*, Ambulacra in which lancet-plates (*l*) only are preserved; *d*, *e*, Ambulacra intact; lancet-plate concealed by side-plates (after Etheridge and Carpenter).

The form and arrangement of the spiracles is extremely variable; they may be round or slit-like; they may consist of ten separate openings, or those of the same pair may be confluent with one another; and the posterior pair may be fused both with each other and with the anus, in which case the fifth or posterior spiracle is considerably larger than the others. *Granatocrinus*, *Pentremites*, *Pentremitidea*, etc. (Fig. 314, *A*), are examples of the latter case; *Granatocrinus* having five circular orifices with tube-like projections, while in *Pentremites* and *Pentremitidea* the four smaller spiracles are divided into two compartments by the terminal median ridge of the deltoids. The posterior

spiracle in the two latter genera is divided by a duplicate ridge into three compartments; of these the middle one enters the inner cavity, and the two outer ones communicate with the hydrospires by means of the hydrospire canal. In *Troostocrinus*, *Schizoblastus*, and *Cryptoblastus* (Fig. 313, *D*) the posterior spiracles are confluent with the anus, while those of the four regular sides are separated. *Elaeacrinus*, *Mesoblastus*, and *Acentrotremites* have ten separate spiracles, and a large, distinct anal aperture. The typical *Codasteridae* (*Codaster* and *Phaenoschisma*), in which the hydrospires are exposed externally, have no spiracles and no hydrospire canal. *Orophocrinus* (Fig. 313, *B*) has ten elongate clefts extending along the sides of the ambulacra; but these are in reality the unclosed portions of the radial sinuses, and correspond to the open hydrospire canals of *Pentremites*, which are apparent upon the removal of the side-plates.

The ambulacra are usually depressed below the general level of the calyx, but are sometimes raised above it, or they may be placed in the same plane with it. They vary in form from narrow linear to broad petaloid, and are considerably complicated in structure (Fig. 315). The centre of each ambulacrum is occupied by the *lancet-plate*, a long, narrow piece, pointed at both ends, which extends to the full length of the fields. Its proximal end is inserted between the deltoids, and takes part in the lip around the summit-opening. The upper surface of the plate is excavated along the median line, and forms an open, well-defined groove, which conducts to the mouth, and in all probability represents the food-groove. The interior of the plate is traversed by an axial canal, which communicates by means of the ambulacral opening with an oral ring belonging to the water-vascular system. In a number of forms (*Pentremites*, *Orophocrinus*) there is to be seen a second, smaller, and extremely thin plate underlying the median portion of the first; this is called the *under lancet-plate*.

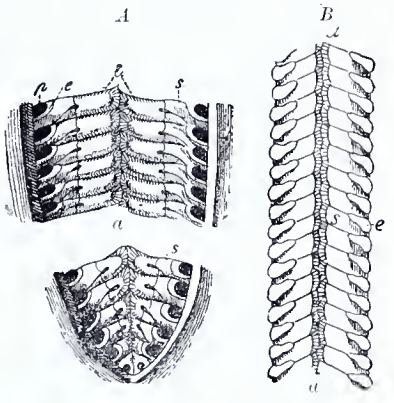

FIG. 315.

A, *Pentremites pyriformis*, Say. Portion of an ambulacrum, exhibiting the lancet-plate (*l*); median food-groove of the same (*a*); side-plates (*s*); outer side-plates (*e*); and marginal pores (*p*). $^5/_1$ (after E. and C.) *B*, Ambulacrum of *Elaeacrinus*. Lettering as in *A* (after Roemer).

The lancet-plate rarely occupies the full width of the ambulacral field, and the spaces between its lateral edges and the sides of the radial sinus are either wholly or partially covered by a row of small, horizontally elongated *side-plates* ("*pore-plates*" of Roemer). In *Pentremites*, *Orophocrinus*, and other genera, an additional series of still smaller pieces, called the *outer side-plates* ("*supplementary pore-plates*" of Roemer), are placed between the side-plates and the walls of the radial sinus. *Pentremites* and *Cryptoschisma* have the entire upper surface of the lancet-plate exposed to view, and the side-plates are situated alongside of it in the same plane. But in other forms the lancet-plate is wholly, or to a very large extent, concealed by the side-plates (Fig. 315, *B*), so that as a rule only a small space along the food-groove is visible. The sutures between the side-plates are indicated by shallow, horizontal grooves, which are continued as superficial markings over both halves of the lancet-plate as far as the median ambulacral groove. These crenulations, it should

be noted, are frequently effaced in weathered specimens (Fig. 315, *A* and *B*).[1] Small pit-like depressions, or small tubercles, which are observable on the side-plates, indicate the places where the appendages or *pinnules* were formerly attached. These are only exceptionally found intact, but when preserved they completely conceal the ambulacral fields, and extend upward above the summit of the calyx (Fig. 316). They vary considerably in length, even among species belonging to the same genus.

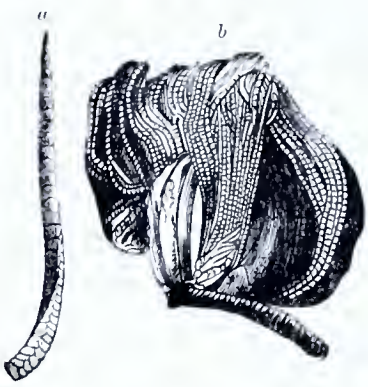

Fig. 316.

a, Pinnule of *Pentremites*, enlarged; *b*, *Granatocrinus Norwoodi*, O. and S., with perfectly preserved pinnules (after Meek and Worthen).

Fig. 317.

Pentremites sulcatus, Say. Sub-Carboniferous; Illinois. Transverse section of calyx at about 1/3 the height of the ambulacral fields. × 1 1/2. *hy*, Hydrospires; *l*, Lanect-plate; *p*, Pore-plates; *r*, Radials.

In most Blastoids the side-plates, or the outer side-plates when such are present, are pierced by *marginal pores* (or *hydrospire pores*), which communicate with the hydrospires. The pores are situated at the extreme outer margins of the plates, at the end of the lateral ridges, and alternate in position with the sockets of the pinnules. They are present in all forms,

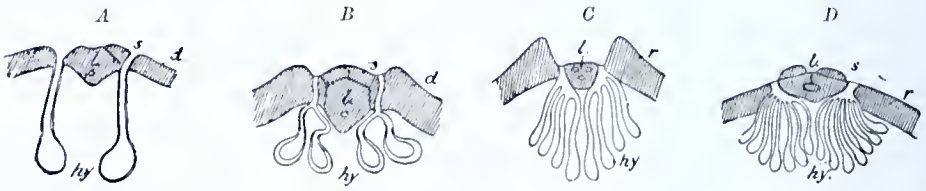

Fig. 318.

Transverse sections through the ambulacral fields, showing various forms of hydrospires. *A*, *Granatocrinus Derbyensis*. *B*, *Granatocrinus Norwoodi*. *C*, *Metablastus lineatus*. *D*, *Orophocrinus verus*. All sections enlarged (after Etheridge and Carpenter).

having the hydrospires concealed within the calyx; but are absent in the *Codasteridae*, in which the hydrospires are wholly or in part exposed on the outer surface.

The *hydrospires* are bundles of flattened, lamellar tubes, extending under-

[1] [According to Wachsmuth these markings are not a mere ornamentation; but the ridges constitute the sides, and the depressions the floors of a series of small ducts leading from the pinnules to the median ambulacral groove. In a number of excellently preserved specimens observed by this distinguished author (*Pentremites*, *Orophocrinus*, and *Schizoblastus*), not only the longitudinal groove, but also the side grooves throughout the entire field were roofed over by alternately arranged, very minute plates, extending all the way to the pinnules. The arrangement of the side ducts, their upward curvature on approaching the main canal, and their relations to the pinnules, leaves scarcely a doubt that they were closed food-grooves serving to conduct nutriment from the pinnules to the mouth.

It is questionable whether the term "pinnules" is strictly appropriate as applied to the appendages of Blastoids, for while the latter evidently performed the function of arms, it is by no means certain that they discharged the ova, which is the special office of pinnules in Crinoids. The statement that the appendages are frequently biserial does not agree with the observations of Wachsmuth. All the specimens examined by this writer are uniserial, but the ossicles are sometimes sharply wedge-shaped, and interlock to a slight extent from opposite sides, thus simulating a biserial arrangement.—Trans.]

neath the lancet- and side-plates, in a direction parallel with the boundaries of the ambulacral fields. They begin at the lower end of the ambulacra, and terminate in the hydrospire canals, of which the spiracles form the external apertures. When the spiracles are confluent, the canals of adjacent groups of hydrospires enter the same opening. The hydrospires are suspended in the majority of forms along the walls of the body-cavity (*Pentremites*), (Fig. 317), being attached either to the outer margins of the under lancet-plate or to a separate piece known as the *hydrospire plate* (*Granatocrinus*, *Mesoblastus*, and *Cryptoblastus*). *Pentremites* has from four to nine hydrospires in each group; *Granatocrinus* two, or exceptionally one; *Troostocrinus* and *Mesoblastus* generally three, and *Orophocrinus* from five to seven (Fig. 318, *A* to *D*). In *Phaenoschisma* and *Codaster* (Fig. 323) the tubes open externally by slits piercing the radials and deltoids and running parallel with the ambulacra.

The functions of the hydrospires can only be surmised, but they are supposed to have served for respiration; they correspond doubtless to the pectinated rhombs and calycine pores of the Cystideans and to the respiratory pores of Crinoids. It is probable that water was admitted to the hydrospire sacs through the marginal pores, and was discharged through the spiracles. Roemer and Forbes have suggested that the hydrospires may also have performed reproductive functions. Ludwig has called attention to the resemblance between the genital bursae of *Ophiuroids* and the slit-like spiracles in *Orophocrinus;* his theory is that the hydrospires served both for purposes of respiration and for the discharge of genital products, a view which was also shared by Carpenter.

The *stem* in Blastoids is preserved only in exceedingly rare instances. It is round, provided with a small axial canal, and composed of short joints, which apparently multiplied in a similar manner as in the Crinoids. In *Orophocrinus* and *Pentremites* it has been traced for a length of 15 cm. without reaching the end; and in the latter form it has occasionally been found with a few, comparatively heavy, radicular cirri.

It has frequently been claimed, owing to the superficial resemblance of their ambulacral areas, that the Blastoids and Echinoids are mutually related; but such presumptions are founded upon a total misconception of the value of external characters. The construction of the calyx, the presence of pinnules, and the stemmed condition, are features which identify them unmistakably as *Pelmatozoa;* and their nearest relatives under this group are the Cystideans. The parallelism between the ambulacral fields of the one class and the recumbent arms, apparently soldered on to the calyx of the other, is self-evident. The hydrospires of Blastoids correspond to the pore-rhombs of Cystideans, as has already been remarked; and the position of the mouth and anus is the same in both types. The Blastoids constitute a peculiar, but, on the whole, a very well-defined group, which is now regarded as of equal rank with the Crinoids and Cystids.

Blastoids have not been recognised as such, up to the present time, in strata lower than the Silurian; but it is possible that several genera occurring in the Ordovician of North America and Russia (*Blastoidocrinus*, *Asteroblastus*, etc.), which are now referred to the Cystids, may eventually be transferred to the *Blastoidea*. The only known Silurian form is *Troostocrinus*, which occurs sparsely in the Niagara Group of North America. Several genera are represented in the Devonian, being distributed in both Europe and America, but

the climax of Blastoid development takes place in the Sub-Carboniferous of North America. Some of the beds of the Kaskaskia Group are fairly charged with their remains, which as a rule are excellently preserved; but above this horizon no traces of them have as yet been discovered. Nineteen genera, comprising upwards of 120 species, are recognised by Etheridge and Carpenter in their admirable monograph.

Order 1. REGULARES. Etheridge and Carpenter.

Pedunculate Blastoids with a symmetrical base, in which the radials and ambulacra are all equal and similar.

Family 1. Pentremitidae. d'Orbigny.

Base usually convex, and often much elongated. Spiracles five, but sometimes more or less completely divided by a median septum, and bounded proximally by the uppermost side-plates. Lancet-plate either entirely visible or partially covered by side-plates which extend to the margins of the ambulacra. Hydrospires concentrated at the lowest part of the radial sinus. Devonian and Sub-Carboniferous.

Pentremites, Say. Calyx usually ovate or pyriform, with elongate, subtruncate base. Ambulacra broad, sub-petaloid. Lancet-plate wholly exposed, and resting below on an under lancet-plate. Side-plates and outer side-plates numerous, the former abutting against the edges of the lancet-plates. Hydrospires three to nine; spiracles single, or occasionally double; the two of the posterior side confluent with the anus, and forming with it a single large orifice. Summit covered by numerous spines, placed closely against one another so as to form a pyramid, which completely covers the summit and the greater portion of the spiracles. Excessively abundant in the Sub-Carboniferous of North America (St. Louis and Kaskaskia Groups), but not identified in Europe. *P. Godoni*, Defrance, and *P. pyriformis*, Say, are the most familiar species.

Fig. 319.

Pentremites Godoni, Defr. Sub-Carboniferous; Ill. (Nat. size.)

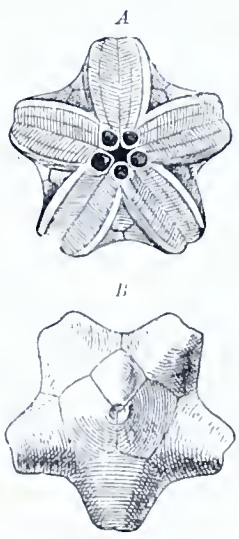

Fig. 320.

Pentremites sulcatus, Roem. Sub-Carboniferous; Ill. *A*, Summit aspect. *B*, Base.

Pentremitidea, d'Orb. Calyx clavate-pyramidal, with elongate, usually conical base, and truncate or convex upper face. Ambulacra narrow, short; lancet-plate more or less completely concealed by side-plates. Deltoids very small, generally confined to the upper face of the calyx, and seldom visible in a side-view. Spiracles and hydrospires as in the preceding. Lower and Middle Devonian; Eifel, Ardennes, Spain, Great Britain, and North America. *P. Pailletti*, de Vern.; *P. Eifelianus*, Roemer; *P. clavatus*, Schultze.

Mesoblastus, E. and C. Calyx oval to globose, with concave to protuberant base. Radials long, deltoids small, short, unequally rhombic. Ambulacra

very narrow, extending to the base. Spiracles, as a rule, distinctly double, but sometimes incompletely divided. Lancet-plate perfectly, or for the most part, concealed by side-plates. Carboniferous; Belgium, England, North America. *M. crenulatus*, Roemer.

Family 2. **Troostoblastidae.** Etheridge and Carpenter.

Ambulacra narrow, linear, deeply impressed, descending outward from the summit. Deltoids confined to the narrow upper end, invisible externally, except the posterior one in Troostocrinus. Lancet-plate entirely concealed by side-plates. Spiracles distinct, represented by lineal slits at the sides of the deltoid ridge, and not bounded by side-plates. Silurian to Sub-Carboniferous (Warsaw Group).

Troostocrinus, Shum. (Fig. 321). Calyx narrow, elongate, somewhat fusiform, with contracted, subtruncate, or slightly convex upper face. Ambulacra short. The four anterior deltoids overlapped by the radia limbs; the posterior one much larger than the rest, and appearing externally. Posterior spiracles confluent with the anus. Silurian (Niagara Group); North America.

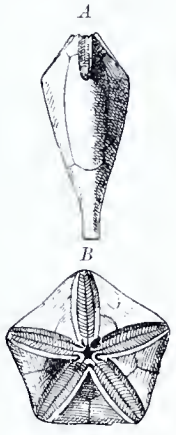

Fig. 321.

Troostocrinus Reinwardti, Troost sp. Silurian; Tenn. (after Roemer). *A*, Calyx from one side (nat. size). *B* Summit aspect (enlarged).

Metablastus, E. and C. Like the preceding, but all the deltoids equal, and the two posterior spiracles not confluent with the anus. Spiracle slits ten in number; hydrospires four to each side of an ambulacrum. Silurian to Sub-Carboniferous.

Tricoelocrinus, M. and W. Calyx pyramidal, broadest below and narrowing upwards; when seen from above or below, strongly pentagonal in outline, owing to the projecting and carinated character of the radials. Deltoids small; ambulacra long, and extremely narrow. Spiracles ten, distinct; anus large. Hydrospires small, enclosed within the substance of the forked plates. Sub-Carboniferous.

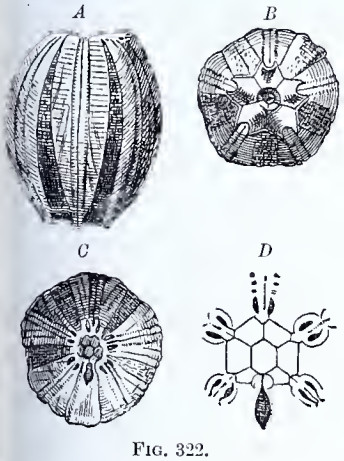

Fig. 322.

Elaeacrinus Verneuili, Troost sp. Lower Devonian; Columbus, O. (after Roemer). *A*, Side-view of calyx. *B*, Base. *C*, Ventral surface. *D*, Same, enlarged.

Family 3. **Nucleoblastidae.** Etheridge and Carpenter.

Calyx usually globular or ovoidal, with flattened or concave base, and linear ambulacra extending the whole length of the calyx. Spiracles distinctly double, and chiefly formed by the apposition of notches in the lancet-plate and deltoids. Devonian and Sub-Carboniferous.

Sub-Family A. Elaeàcrinidae. Etheridge and Carpenter.

Posterior deltoid divided into two parts by an anal plate. Anus distinct from the posterior spiracles.

Elaeacrinus, Roemer (*Nucleocrinus*, Conrad), (Fig. 322). Basals small, inconspicuous, sometimes hidden within the columnar cavity. Radials small,

with very short limbs. Deltoids greatly enlarged and elongated, forming over two-thirds of the entire calyx; the posterior one wider than the others, and divided by a large anal plate. Lancet-plate exceedingly long and narrow, partly exposed. Side-plates numerous; hydrospires two to each side of the ambulacra. Summit covered by comparatively large orals, asymmetrically arranged and forming a flattened disk which completely closes the peristome. Devonian; North America.

Sub-Family B. Schizoblastidae. Etheridge and Carpenter.

The posterior deltoid not divided by an anal plate. Posterior spiracles may be fused with the anus.

Schizoblastus, E. and C. Calyx resembling that of *Granatocrinus* in form. Basals almost always confined to the lower face of the calyx; deltoids of variable size, but always visible in a side view. Hydrospires one to four to each ambulacrum. Spiracles small, slit-like, placed between the lancet-plates and deltoid ridges; the posterior pair sometimes confluent with the anus. Sub-Carboniferous; Ireland and North America.

Cryptoblastus, E. and C. Calyx sub-globose, with a flattened or slightly hollowed base. Basals and deltoids small. Lancet-plate separated from the radials by a hydrospire-plate, which does not extend above the radio-deltoid suture; but above this line the lancet-plate meets the deltoids without leaving any hydrospire-pores. Spiracles round, distinctly double at four of the sides, but those of the posterior side confluent with each other and with the anus. Summit covered by numerous, irregularly arranged small pieces. Sub-Carboniferous; North America.

Acentrotremites, E. and C. Calyx elliptical, with broad pentagonal lower face. Radials large, taking up three-fourths of the height of the calyx. Deltoids unequally rhombic, each notched by two spiracles at the ends of the radio-deltoid suture. Anal opening situated close to the summit in the posterior deltoid. Ambulacral edges of the deltoids without hydrospire pores. Sub-Carboniferous; Great Britain.

Family 4. **Granatoblastidae.** Etheridge and Carpenter.

Calyx globular or ovoidal, with flattened or concave base, and long linear ambulacra. Spiracles five, piercing the deltoids, or ten, grooving their lateral edges. Sub-Carboniferous.

Granatocrinus, Troost (Figs. 316, 318, *A*, *B*). Calyx ovate to globose. Lower face from slightly concave to deeply funnel-shaped; interradial areas more or less depressed. Basals small, generally concealed in the central columnar cavity. Radials very variable in size, often long, and invariably turned in below to assist in forming the base. Deltoids also variable; usually unequally rhombic, but sometimes triangular; the anal deltoid frequently differing from the others. Ambulacra nearly parallel-sided, always impressed within the sinuses at their proximal ends. Lancet-plates narrow, not filling the sinuses, and more or less exposed throughout two-thirds of the ambulacra. Side-plates transversely elongated; outer side-plates generally well developed. Hydrospires pendent, usually but two or three folds on each side of an ambulacrum; the inner one forming a well-defined hydrospire-plate. Spiracles

five, piercing the apices of the deltoids. Posterior spiracle larger, including the anus. Summit closed by minute pieces which rarely exhibit any definite arrangement. Sub-Carboniferous; England and North America.

Heteroblastus, E. and C. Resembling the preceding in form and proportion of its component parts. The proximal ends of the deltoids produced in short spine-like processes, at the base of which minute lateral openings, one to each deltoid, are visible. These openings lead into gutter-like channels excavated in the substance of the plates for the reception of the proximal ends of the two hydrospire-canals. Radial sinuses wide, their edges sloping gently downwards to the slightly petaloid ambulacra. Carboniferous Limestone; England.

Family 5. **Codasteridae.** Etheridge and Carpenter.

Base usually well developed, and sometimes very long. Ambulacra without marginal pores. Hydrospire-slits either wholly exposed, piercing the calyx plates along the sides of the radial sinuses, or restricted portions of them remain open as spiracles, while the remaining parts are concealed by the ambulacra. Devonian and Lower Sub-Carboniferous.

Codaster, M'Coy (*Codonaster*, Roemer), (Fig. 323). Calyx inverted, conical, or pyramidal. Upper face broad, truncate, or gently convex; section, as a rule, distinctly pentagonal. Basals forming a conical or triangular cup,

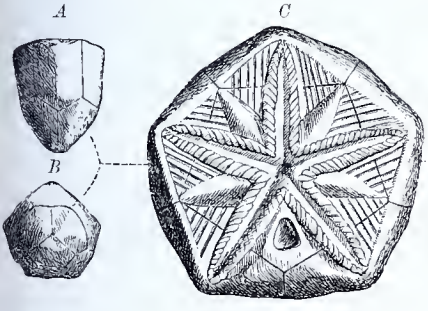

Fig. 323.

Codaster acutus, M'Coy. Carboniferous Limestone; Derbyshire. *A*, Side-view of calyx. *B*, Base. *C*, Ventral aspect, enlarged (after Roemer).

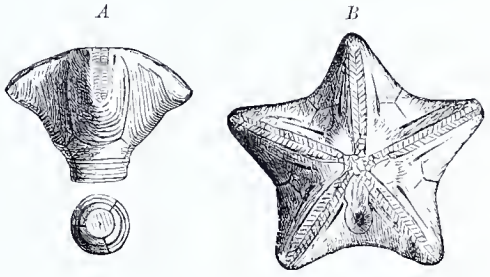

Fig. 324.

Orophocrinus stelliformis, O. and S. sp. *A*, Calyx and base of the natural size. *B*, Ventral surface enlarged (after Meek and Worthen).

usually deep. Radials large, their limbs bent inward horizontally, to assist in forming the truncated upper face of the calyx, and never deeply excavated by the sinuses. Deltoids wholly confined to the upper face, as are also the ambulacra. The latter are petaloid, or narrow and linear; lancet-plate, as a rule, deeply excavated for the side-plates. Spiracles absent, hydrospires pendent, arranged in eight groups, two in each of the four regular interrays, but wanting in the anal one. The tubes open externally by a variable number of elongated slits, which are separated by intervening ridges; one or more of them may be partially concealed by the overlapping side-plates. Anus large, ovate, or rhombic, and piercing the posterior deltoid. Ornament consisting of fine lines arranged parallel to the margins of the plates. Silurian to Sub-Carboniferous; Europe and North America.

Phaenoschisma, E. and C. Calyx resembling that of *Codaster* in general form, but with ten groups of hydrospires instead of eight. Radials bear each three more or less distinct folds diverging from the lip; sinuses wide and

deep, generally with steep sides. Deltoids small, confined to the truncated upper face of the calyx. Lancet-plates in all but one species (*P. caryophyllatum*) concealed by the side-plates; outer side-plates very small. Spiracles rarely present. Hydrospires pendent, and opening externally by a series of elongate slits with intervening ridges, distributed in sub-parallel order on the sloping sides of all the radial sinuses. The slits are only partially covered by the ambulacral plates, and are sometimes visible for their entire length. Lower Devonian; Spain. Sub-Carboniferous; Europe and North America.

Cryptoschisma, E. and C. Calyx elongated, with a broad, flat, truncated upper face. Radial sinuses wide and open, their sloping sides pierced by hydrospire-slits, which are completely concealed by broad, petaloid ambulacra. Spiracles small, single, or more rarely double; in the latter case the posterior pair are confluent with the anus. Represented by the solitary species *C. Schultzi*, d'Archiac et de Vern. Lower Devonian; Spain.

Orophocrinus, v. Seebach (*Codonites*, M. and W.) Calyx balloon-shaped to truncate ob-pyramidal, with more or less concave upper face. Section distinctly pentagonal or stellate. Ambulacra narrow, linear to sub-petaloid. Deltoids generally visible in side-view, the posterior one wider than the others. Spiracles ten, varying from wide clefts along the sides of the ambulacra to narrow slits at their upper ends; the posterior pair separate from the anus. Hydrospire-slits almost completely concealed, being concentrated at the bottom of the radial sinuses. Stem round, composed of short, nearly equal joints. Pinnules extending to nearly twice the height of the calyx, of uniform thickness throughout, and composed of sharply cuneate pieces interlocking from opposite sides; ventral furrow wide, and covered by small pieces. Sub-Carboniferous; Great Britain, Belgium, and North America.

Order 2. IRREGULARES. Etheridge and Carpenter.

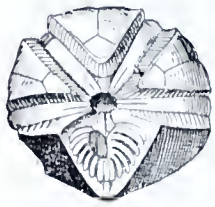

Fig. 325.

Eleutherocrinus Cassedayi, Shum. and Yand. Lower Devonian; Ky. Ventral surface, $^2/_1$. (After E. and C.)

Non-pedunculate Blastoids in which one ambulacrum and the corresponding radial are different in form and size from the others.

Family 1. Astrocrinidae. T. and T. Austin.

This family embraces the three rare genera—*Eleutherocrinus*, Shum. and Yandell (Fig. 325), occurring in the Devonian of North America; *Astrocrinus*, Austin; and *Pentephyllum*, Haughton. The two latter forms are found in the Carboniferous Limestone of England and Scotland.[1]

[1] [The substance of the editorial notes in brackets occurring throughout the Crinoid and Blastoid chapters has all been very kindly communicated by Mr. Charles Wachsmuth. Much of this matter embodies the results of original and as yet unpublished observations. Special acknowledgments are therefore due to Mr. Wachsmuth, without whose generous assistance the above-named chapters of the present edition would have been imperfect in many respects.—Trans.]

Sub-Branch II. **Asterozoa.** Leuckart.[1]

Stemless Echinoderms with depressed, pentagonal, or star-shaped body, consisting of a central disk and five or more rays (or "arms"). Mouth inferior and central in position. Ambulacral tube feet restricted to the under surface of the rays. Internal skeleton pieces of the ambulacra articulated together like vertebrae, or apposed like the rafters of a pent-house. Integument coriaceous, strengthened by small, irregular, loosely united calcareous plates, some of which bear spines, bristles, protuberances, or papillae; the whole constituting a covering of the most varied kind.

The *Asterozoa* comprise the two classes of *Asteroidea*, or Star-fishes; and *Ophiuroidea*, or Brittle-stars and Sand-stars. In both types the body consists of a central disk containing the principal viscera, and giving off five or more radiating processes or arms. The radiating ambulacral vessels are protected by an internal skeleton consisting of a double row of calcareous bodies (*ambulacral ossicles*), the components of each pair being separated and movable to a slight extent in the *Asteroidea*, but are welded together so as to form a series of disks in the *Ophiuroidea*. The ambulacral grooves are open in the *Asteroidea;* but in the *Ophiuroidea* they are covered by dermal plates, and the tube feet project at the sides of the arms. The integumentary skeleton appears leathery on the dorsal surface, but is generally strengthened by innumerable small calcareous bodies, on some of which are placed movable spines or bristles.

Fossil Asterozoans are found as far back as the Cambrian era, and are represented continuously down to the present time. They are of rather uncommon occurrence, and are found, as a rule, in calcareous or arenaceous strata which have been deposited in shallow water. The Asterozoans are the most homogeneous and most persistent type of all the *Echinodermata*. Both the *Asteroidea* and *Ophiuroidea* are represented in the Ordovician and Silurian by well-differentiated forms which do not differ materially from those now living. The only noticeable difference is that many of the Palaeozoic Asterozoans exhibit an alternate arrangement of the ambulacral ossicles, these being developed in all recent species in a double row, with the ends directly apposed. The more or less disjunct condition of the vertebral ossicles in Palaeozoic Ophiuroids must be regarded as an embryonic character.

[1] Literature :

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The ventral position of the madreporite in Palaeozoic Star-fishes and the absence of mouth shields in Palaeozoic Ophiuroids point to an intimate relationship between the two groups; and this inference is still further confirmed by our knowledge of several recent and fossil intermediate forms (*Astrophiura*, *Protaster*, *Brisinga*, etc.)

If one places a Star-fish or Brittle-star with the mouth uppermost, it will be seen that the actinal side corresponds with the tegmen, and the central disk with the base of a Pelmatozoan. When oriented in this manner, the position of the principal organs (ambulacral, circulatory, and nervous systems) is the same in both groups. The homology between the arms of an Asterozoan and those of a Crinoid or Cystid, or the ambulacral fields of a Blastoid, can also hardly be doubted. But efforts to interpret a homology between plates of the dermal skeleton as developed in either group have been only partially successful; the reason being that these structures became variously modified and specialised throughout the different classes at an extremely early period.

A comparison of the ontogenetic stages passed through by the *Pelmatozoa* and *Asterozoa* reveals nothing definite in regard to their close relationship; but the identity in position of the principal viscera argues strongly in favour of their common origin. The Asterozoans are most nearly comparable with certain of the Cystideans (*Agelacrinus* and the *Callocystidae*). But that they are the direct descendants of the *Cystoidea* appears very improbable, for both geological and morphological reasons. The fact is, that both types appear simultaneously and in a high state of development, each being totally distinct from the other, as far back as the Cambrian.

Class 1. OPHIUROIDEA. Gray. Brittle-stars.[1]

Asterozoans having a more or less sharply defined central disk containing a simple digestive cavity which does not radiate into the slender rounded arms, and has no anal opening. Reproductive organs confined to the disk. Arms with an axis composed of jointed calcareous disks, encased with plates or covered with a leathery skin, and destitute of open ambulacral grooves. Madreporite constantly on the actinal (oral) side of the disk.

Ophiuroids are distinguished from the typical Star-fishes by their cylindrical flexible arms, which are sharply separated from the central disk, and do not contain diverticula of the alimentary canal nor of the sexual organs.

[1] Literature:

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The arms serve as locomotive organs, and are either elegantly plated (*Ophiureae*), or protected by a coriaceous skin, in which minute granules and scales are embedded (*Euryaleae*). When plated, the covering consists typically of four rows of calcareous plates, known as the upper, lower, and side arm-plates (*Scutella dorsalia*, *ventralia*, and *lateralia*), (Fig. 326, *A*). The lateral or *adambulacral* plates usually carry rows of mobile spines.

The greater part of the interior of the arms is occupied by a linear series of jointed, vertebrae-like sections called the *vertebral ossicles* or *arm-bones*, each of which is made up of two ambulacral pieces soldered side by side (Fig. 326, *B*, *C*). The halves of the first two vertebral disks are swung laterally into the interbrachial space, being fused together to form the mouth angle. The remainder of the arm-bones are movably articulated with one another by means of bosses which project from the centres of both surfaces, the interspaces being filled with muscles. The entire series is incised inferiorly along the median line for the reception of the radiating water-tube, beneath which

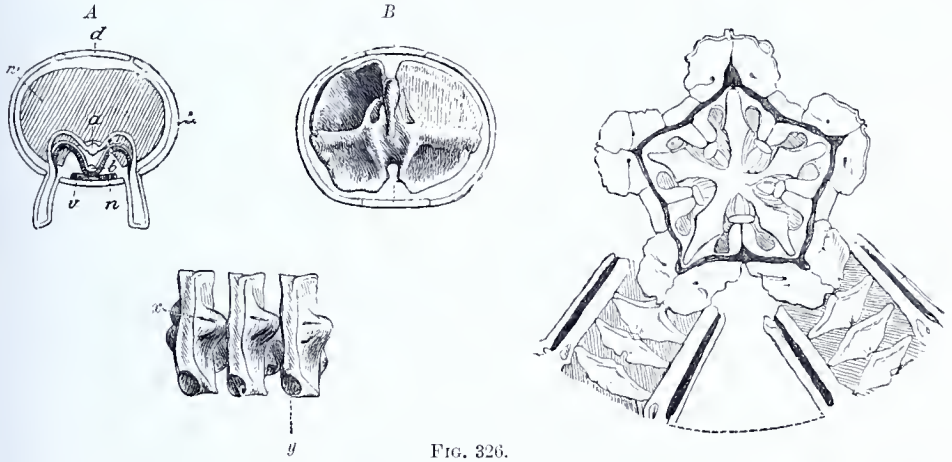

FIG. 326.

A, Vertical section of an Ophiuran arm. *w*, Vertebral ossicle; *a*, Ambulacral vessel, with side-branches leading into the tube feet; *b*, Blood-vessel; *n*, Nerve-cord; *v*, Ventral or lower arm-plate; *l*, Side-plates; *d*, Dorsal plate. *B*, Vertebral ossicle, seen from the inward side, with surrounding arm-plates. *C*, Row of vertebral ossicles viewed from the side, and slightly enlarged; *x*, Apertures where the branches of the ambulacral vessel enter and emerge from the arm-bones; *y*, Depressions for the insertion of intravertebral muscles. *D*, Mouth-frame of an Ophiuran, with the proximal vertebral ossicles. The heavy lines bordering the arms represent the bursal fissures; the dark pentagon in the centre marks the course of the nerve-ring.

runs the radiating blood-vessel and nerve cord, the whole being closed in by the integument. The radiating ambulacral vessel gives off a pair of lateral branches in each arm ossicle which pierce the bone itself, and supply the tentacle-like tube feet with water. The tube feet are without either ampullae or terminal suckers, and the orifice of the plates through which they protrude is often protected by one or more minute tentacle scales (*papillae ambulacrales*), which serve to cover the tentacles when they are drawn in.

On the under side of the disk is seen the central, pentagonal aperture of the *mouth* (Fig. 331), which leads into a large sac-like stomach. The latter terminates blindly, there being no intestine. The body cavity also contains the ambulacral, blood, and nerve rings, as well as the generative glands, whose ducts open into folded pouches or *bursae*. The bursae are arranged in five pairs, one to each interbrachial area, and communicate with the exterior by means of slit-like *bursal fissures*, which skirt the arm bases inferiorly, and are bounded by *genital* or *bursal scales*. Sometimes the fissures are discontinuous

(*Ophiura*), appearing as two slits one behind the other; and in the fossil *Euryaleae* they are often represented by rows of pores.

The integument covering the entire upper surface of the disk and the interbrachial area on the ventral side is frequently beset with calcareous plates; but this scale coat may be covered in turn with a thick skin, or bear spines or granules. A large central plate is sometimes recognisable on the dorsal aspect of the disk, together with five pairs of plates, which, from their position at the points of origin of the arms, are called *radial shields* (*Scutella radialia*, Fig. 328). On the ventral surface of the disk, the inner angle of each interbrachial space is occupied by a single large plate termed the *mouth shield* (*Scutum buccale*), one of which serves as the madreporic body. But in the *Euryaleae* the mouth shields are feebly developed, or may be wanting altogether; and in place of them a madreporite is found in one or all of the interrays. The mouth shields are bounded proximally by a pair of somewhat

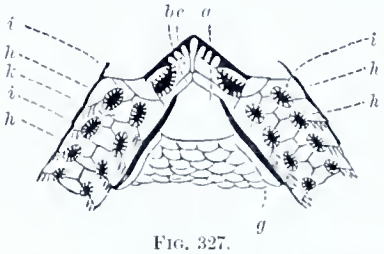

Fig. 327.

Portion of central disk of *Ophioglypha* viewed from the ventral side. *a*, Mouth shield; *b*, Side mouth shield; *c*, Jaws covered by papillae; *g*, Bursal fissures; *h*, Side arm-plates; *i*, Pores for the emission of the tube feet, surrounded with tentacle scales; *k*, Spines.

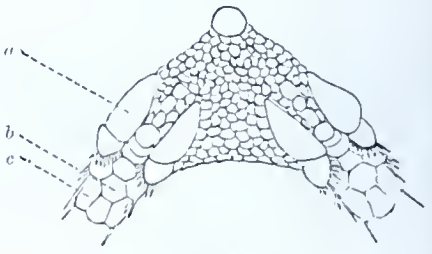

Fig. 328.

Portion of central disk of *Ophioglypha* viewed from the dorsal side. *a*, Radial shields; *b*, Upper arm-plates; *c*, Side-plates.

smaller plates called the *side mouth shields* (*Scutella adoralia*). Finally, within the side mouth shields, and usually pressing against them, are the *jaws* (*Scutella oralia; Mundeckstücke*), which are sometimes covered by the skin or by granulations (Fig. 327). Teeth are constantly present, being attached to the jaw-plates by small muscles.

The *Ophiuroidea* are divided into two orders: *Euryaleae* and *Ophioureae*, both of which have fossil representatives dating as far back as the early Palaeozoic era. For a precise systematic determination it is necessary to know the character of the bursal fissures and the mouth frame; but such evidence is not always obtainable in the case of fossil specimens, owing to imperfect conditions of preservation.

Order 1. EURYALEAE. Müller and Troschel.

Arms dichotomously dividing soon after their origin (exceptionally simple throughout their entire length), capable of being rolled up inwards, and covered with a granulated or finely scaled integument. Mouth shields rudimentary or absent. Genital fissures often represented by rows of pores. A madreporite present in one or all of the interrays. Silurian to Recent.

The Palaeozoic species differ from all of the recent *Astrophytidae* in that radial shields are not present, and that the arms bear a row of simple marginal spines on the ventral aspect.

Eucladia, Woodw. Disk granulated. Each of the arms giving off five pairs of secondary branches, which increase in size outwards. One large madreporite present. Silurian; England.

Onychaster, Meek and Worth. Central disk round, small. Arms five, simple, long, and covered with a tuberculous integument, in which fine scales are embedded. Sub-Carboniferous; North America.

? *Helianthaster*, Roemer. Disk large, granulated. Arms sixteen, long, broad, and covered with a granulated integument. Lower Devonian; Bundenbach.

? *Euryale*, Lam. It is possible that the rough impressions described by Quenstedt as *Euryale liasica*, from the Angulatus Bed of Nürtingen (Lias α), also belong here.

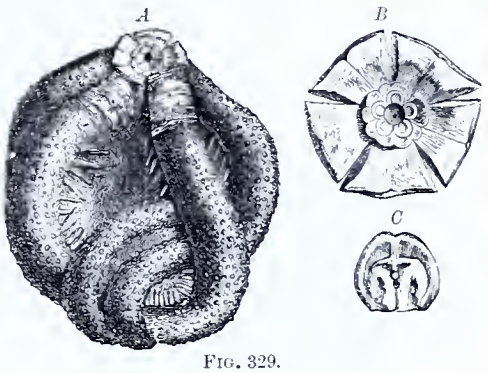

Fig. 329.

Onychaster flexilis, M. and W. Sub-Carboniferous; Crawfordsville, Ind. (after Meek and Worthen). Individual of the natural size with rolled up arms; the dorsal covering of the ventral disk is removed, exposing the mouth frame. *b*, Mouth frame enlarged, viewed from above; *c*, vertebral ossicle, enlarged.

Order 2. OPHIUREAE. Müller and Troschel.

Arms invariably simple, incapable of being rolled up towards the mouth, and, as a rule, cased with four series of integumentary plates. Silurian to Recent.

Mouth shields are well developed in recent forms, one of them serving as a madreporite; but they are absent in all fossil species.

Sub-Order 1. OPHIO-ENCRINASTERIAE. Stürtz.

Arms without ventral shields, the lateral elements of the vertebral ossicles disjunct, and alternately arranged. Mouth shields absent. Disk covered with skin or fine scales, sometimes spinous. Silurian and Devonian.

To this sub-order belong the following genera:—*Protaster*, Forbes, from the Silurian of England and America. *Taeniaster*, Billings; Silurian. *Eugaster*, Hall; Devonian. *Palaeophiura* and *Bundenbachia*, Stürtz; Lower Devonian.

Sub-Order 2. PROTOPHIUREAE. Stürtz.

Arms without dorsal, sometimes without ventral shields. Elements of the vertebral ossicles placed opposite one another, and more or less anchylosed. Disk without either radial shields, mouth shields, or genital scales. Silurian and Devonian.

The sub-order is divided by Stürtz into three groups, comprising the following species:—

(*a*) *Ophiurina Lymani*, Stürtz. Lower Devonian; Bundenbach.

(*b*) *Protaster Miltoni*, Salter. Silurian; England. *Furcaster palaeozoicus* and *Ophiurina Zitteli*, Stürtz. Lower Devonian; Bundenbach.

(*c*) *Ophiura primigenia*, *O. Decheni*, and *O. Rhenana*, Stürtz. Lower Devonian; Bundenbach.

Sub-Order 3. EUOPHIUREAE.

Arms with dorsal, lateral, and ventral shields. Mouth shields well developed, one of them serving as a madreporite. Devonian to Recent.

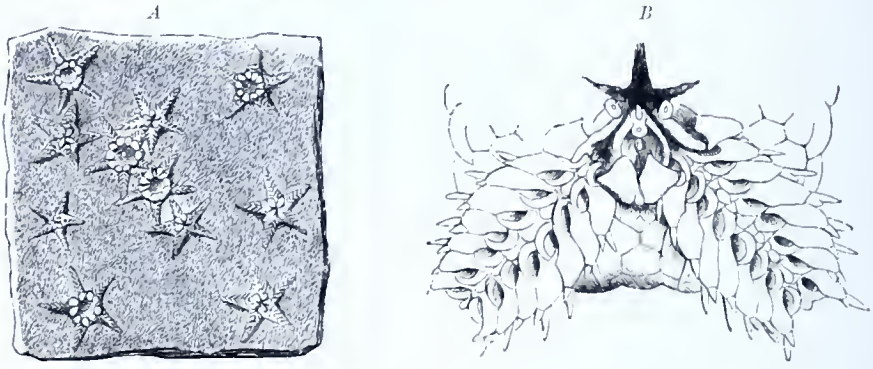

FIG. 330.

Aspidura loricata, Goldf. sp. Muschelkalk; Waschbach, Wurtemberg. *A*, Group of individuals of the natural size (after Quenstedt). *B*, Ventral aspect enlarged (after Pohlig).

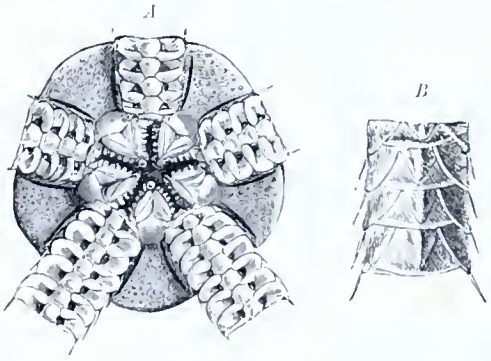

FIG. 331.

Ophioten Kelheimense, Bohm. Lithographic Slates; Kelheim, Bavaria. *A*, Ventral aspect of disk, enlarged. *B*, Dorsal surface of one of the arms. (Both figures enlarged; original in Munich Museum.)

The Ophiuroids of the Mesozoic era are closely related to recent forms, and are all assignable to families now in existence. Most of them have but two bursal fissures in each interradium; but the genus *Ophiura*, Lam. (*Ophioderma*, M. and T.), has four in each interray, and is represented as early as the Trias (*O. Hauchecorni*, Eck; Muschelkalk. *O. Egertoni*, Brod. sp.; Lias).

The genera *Aspidura* (Fig. 330) and *Acrura*, Agassiz, are occasionally abundant in the German Muschelkalk, and certain Liassic Ophiurans also

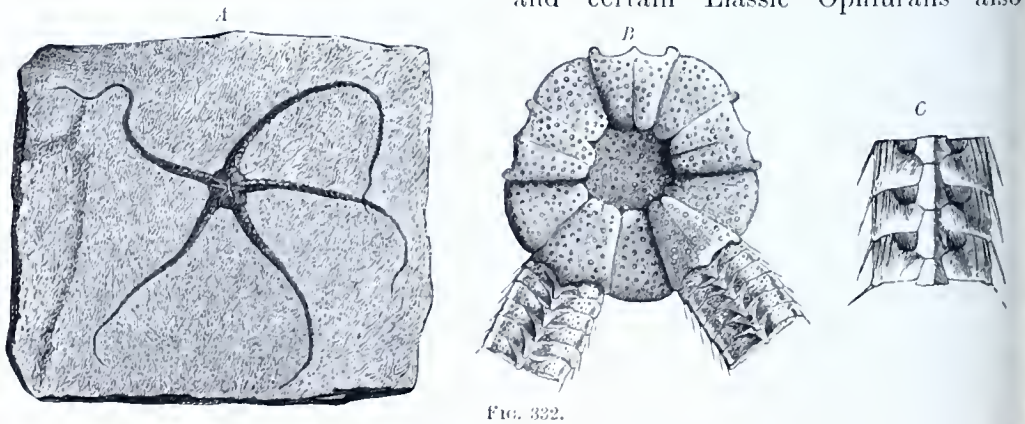

FIG. 332.

Geocoma carinata, Goldf. Lithographic Slates; Zandt, near Solenhofen, Bavaria. *A*, Individual of the natural size. *B*, Dorsal aspect of disk, showing granulations and central depression. *C*, Ventral surface of one of the arms. (Figs. *B* and *C* enlarged.)

lived in herds. In the Lower, Middle, and Upper Jura are found forerunners

of the recent genera *Ophiolepis*, M. and T.; *Ophiocten*, Lütk. (Fig. 331); *Ophioglypha*, and *Ophiomusium*, Lyman. Some of the forms described under the head of *Geocoma*, d'Orb. (such as *G. socialis*, Heller, from the Callovien of La Voulte; or *G. Libanotica*, König, from the Cretaceous of Hakel, Lebanon), are incapable of precise determination; others (such as *G. carinata*, Goldf., Fig. 332) are closely related to the recent *Amphiura*.

Ophiurella elegans, Agassiz, from the Lithographic Slates of Solenhofen, is referred by Lütken to *Ophiocoma*, Agassiz. Other Jurassic and Cretaceous forms which have been described under various generic names are assigned by the same author to *Ophioglypha*, Lyman. Fossil Ophiuroids which do not admit of critical determination are usually grouped together under the general term of *Ophiurites*.

Class 2. ASTEROIDEA. Star-fishes.[1]

Asterozoans whose simple and more or less flattened arms are prolongations of the central disk, and contain the hepatic appendages of the alimentary canal, as well as the generative organs. Ambulacral feet disposed in rows along deep open grooves on the under or actinal surface of the arms.

Star-fishes have typically five arms (but in some cases as many as eight, ten, twelve, twenty, or more), which are prolongations of the central disk, and are not sharply marked off from the same. The integumentary skeleton consists of plates which are either contiguous with one another along their edges, or are united in a reticulate fashion, and covered with a leathery skin. The calcareous plates often bear movable spines or bristles, or they may be tuberculated or granulated. The abactinal surface usually exhibits a central or subcentral anus, and also a madreporite, which is situated in one (rarely two or more) of the interradii. The madreporite is covered with labyrinthic furrows, and is perforated for the admission of water into the so-called *stone canal*, whence it is conveyed into the water-vascular ring surrounding the mouth. The fine pores and protrusive coecal processes (*papulae*), which in the *Phanerozonia* are restricted to the dorsal surface, but in the *Cryptozonia* are distributed over the whole body, serve as respiratory organs, the body fluids being brought into close contact with the oxygenated water.

The mouth occupies the centre of the dorsal surface, and is pentagonal in contour, owing to the projection of five pairs of interradially disposed oral

[1] Literature:

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Fraas, E., Die Asterien des weissen Jura (Palaeontographica, XXXII.), 1886.

plates. Each of the arms is traversed on the under or oral side by a broad and deep furrow, which tapers gradually in passing from the mouth to the tip of the arm, where it is terminated by a simple grooved plate (Fig. 333) called the *ocular plate*. The roof of each ambulacral furrow is formed by two rows of rafter-like, rather elongate, *ambulacral ossicles*, the inner ends of which are held together by muscles (Figs. 334, 335). Running along the centre of the groove on its ventral side are placed in succession the radial water-tube, blood-vessel, and nerve cord. These are all homologous with the like-named organs of Ophiuroids.

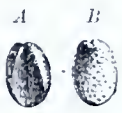

Fig. 333.

Ocular plates of *Pentagonaster*(?) from the Upper Jura of Streitberg. $^2/_1$.

Fig. 334.

Detached ambulacral ossicle of *Pentagonaster* (?) from the Upper Jura of Streitberg. $^1/_1$.

The form of the ambulacral ossicles varies in different genera. In all recent forms the ends are directly apposed against one another in the median line of the ambulacral grooves; but in Palaeozoic forms they are arranged in alternate rows, and are inclined towards one another at a very small angle. Each pair of ambulacral plates is excavated at the sides, so as to give rise by their apposition to a series of small

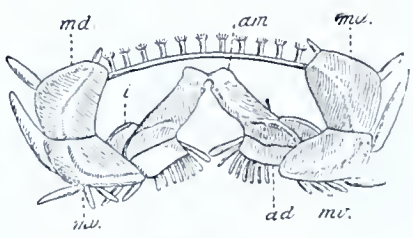

Fig. 335.

Astropecten aurantiacus, Linn. sp. Recent; Mediterranean. Enlarged vertical section of one of the arms. *am*, Ambulacral ossicles; *ad*, Adambulacral plate; *mv*, Infero-marginal plate; *md*, Supero-marginal plate; *i*, Super-ambulacral plate.

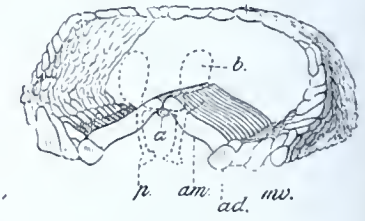

Fig. 336.

Asterias rubens, Linn. Recent; German Ocean. Enlarged vertical section of one of the arms. *am*, Ambulacral ossicles; *ad*, Adambulacral plates; *mv*, Infero-marginal plates; *a*, Radiating water-tube; *b*, Ampullae; *p*, Tube feet.

apertures, through which the distensible tube feet or pedicels are emitted. The latter are the downward prolongations of lateral branches given off by the radial ambulacral vessel; the upward prolongations of the same form small sacs called *ampullae*, by means of which water is forced into the tube feet.

The lower ends of the ambulacral ossicles rest against a series of *adambulacral plates*, and in many forms these are bounded in turn by large *marginal plates* (Fig. 335). *Intermediate plates* are those which are inserted between the infero-marginal plates and the adambulacral plates. By the term *dorsal plates* are understood all calcareous bodies occurring on the dorsal side of the body.

Perfectly preserved Star-fishes are known only from a few localities, such as Bundenbach in Rhenish Prussia, the usual mode of occurrence being in the form of moulds or detached plates. The earliest forms are found in Cambrian rocks.

Sub-Class 1. ENCRINASTERIAE. Bronn.

Palaeozoic Star-fishes with but slightly inclined ambulacral ossicles, their ends meeting alternately in the middle of the ambulacral grooves. Madreporite situated on the oral side of the disk. Cambrian to Carboniferous.

Two principal groups may be indicated in this sub-class, in one of which marginal plates are strongly developed, and in the other they are either absent or rudimentary. So little is known, however, of the complete structure of the majority of Palaeozoic forms, that in the case of some genera it is impossible as yet to determine positively the group in which they should be classed.

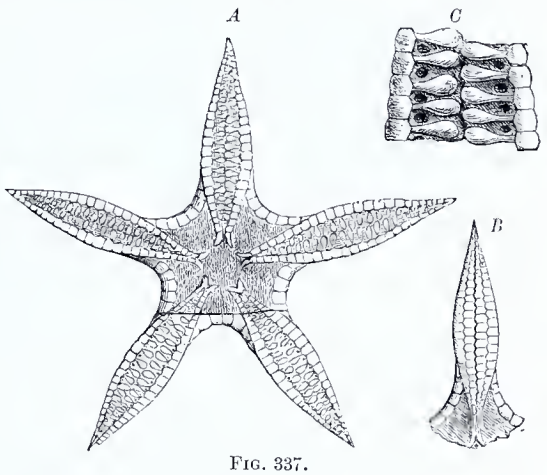

Fig. 337.

Aspidosoma petaloides, Simon. Lower Devonian; vicinity of Niederlahnstein, Nassau. *A*, Ventral aspect, natural size. *B*, Arm viewed from the dorsal side. *C*, Ventral aspect of arm, enlarged (after Simonowitsch).

To the first group belong the following genera: — *Aspidosoma*, Goldf. (Fig. 337). Devonian; Rhenish Prussia. *Palaeaster*, Hall (*Petraster*, Billings; *Archasterias*, Müller), (Fig. 338). Ordovician to Carboniferous; Europe and North America.

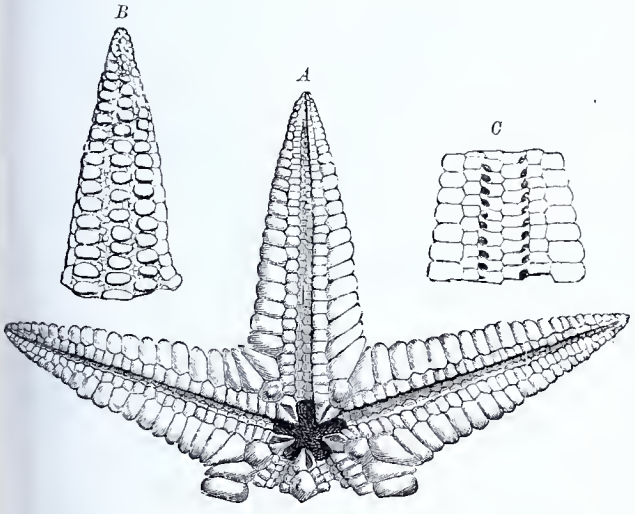

Fig. 338.

Palaeaster Eucharis, Hall. Devonian; Hamilton, New York. *A*, Ventral aspect, natural size. *B*, Dorsal surface of one of the arms. *C*, Diagrammatic view of ventral surface of the arms (after Hall).

Salteraster, Stürtz (*Palaeaster*, Salter, p.p.) Ordovician; England. *Palaeostella*, Stürtz. Lower Devonian; Bundenbach.

Palasterina, M'Coy (Cambrian to Devonian; Europe and North America), should probably be ranked in this group as a transitional form. *Urasterella*, M'Coy (*Stenaster*, Billings, p.p.), (Ordovician; Canada), is also considered by Stürtz as a member of this group.

To the second group belong the genera: *Palaeocoma*, *Bdellacoma*, and *Rhopalocoma*, Salter. Silurian; England. *Loriolaster*, *Cheiropteraster*, and *Palasteriscus*, Stürtz. Lower Devonian; Bundenbach.

Sub-Class 2. EUASTERIAE. Bronn.

Pairs of ambulacral ossicles placed opposite each other, inclined upwards like the rafters of a roof, and united with one another by muscles at their inner ends. Madreporite, except in a few Palaeozoic types, restricted to the dorsal surface. Silurian to Recent.

This sub-class is divided into two orders, depending upon the character of the marginal plates. Both groups make their appearance in the Palaeozoic era, and continue to the present day.

Order 1. PHANEROZONIA. Sladen.

Marginal plates large and highly developed; the supero-marginal and infero-marginal plates contingent. Papulae restricted to the dorsal surface. Ambulacral plates well spaced and usually broad.

Forms apparently congeneric with the recent members of the *Archasteridae* and *Astropectinidae* are represented in the Devonian. *Xenaster*, Simonowitsch, a small, five-armed type from the Lower Devonian of Rhineland, has adambulacral and intermediate plates. A large form from the Devonian of Bundenbach, with five long, depressed arms, rectangular adambulacral plates, and two rows of marginal plates, is regarded by Stürtz as identical with the recent genus *Astropecten*, Linck. (Fig. 335). Numerous species referred to the same genus have been described from the Lias onwards.

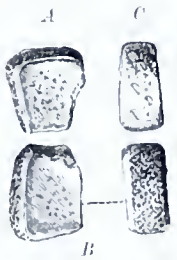

FIG. 339.

Pentagonaster(?) *impressus*, Quenst. sp. Upper Jura; Reichenbach im Thale. *A*, Supero-marginal plate. *B*, Infero-marginal plate. *C*, Plate with supposed pedicellariae (after Quenstedt).

The genus *Luidia*, Forbes, has also been considered to be represented by a form from the Lias. *Plumaster*, Wright, from the Lias, is probably a near ally.

Trichasteropsis, Eck. Central disk large. Arms moderately long, tapering, and covered on the ventral side with spines. Marginal plates rather small, except on the dorsal side at the tips of the arms. Muschelkalk.

Pentagonaster, Linck (*Goniaster*, Ag. p.p.) Body depressed and pentagonal, or with the rays slightly produced. Marginal plates generally few in number, and decreasing in size on approaching the extremity of the ray. Abactinal area covered with rounded or polygonal plates. Cretaceous to Recent.

Metopaster, Sladen (*Goniaster*, Ag. p.p.), (Fig. 341). Distinguished from the preceding by the ultimate supero-marginal plates, which are the largest of the series, and by all the marginal plates having a surrounding border of setae. Cretaceous.

Mitraster, Sladen (*Goniaster*, Ag. p.p.) Cycloid in contour, with supero-marginal plates few in number, and all of nearly the same size. Cretaceous.

Calliderma, Gray. Cretaceous to Recent. *Nymphaster*, Sladen. Cretaceous to Recent. *Pycnaster*, Sladen. Upper Cretaceous; England. *Leptaster*, de Loriol. Jura.

Pentaceros, Linck (*Oreaster*, Müll. and Trosch.), (Fig. 341). Fossil forms

occur with large, tuberculous plates on the abactinal area, which are often armed with powerful spines. Upper Jura to Recent.

Sphaerites, Quenst. Under this title are included detached hexagonal

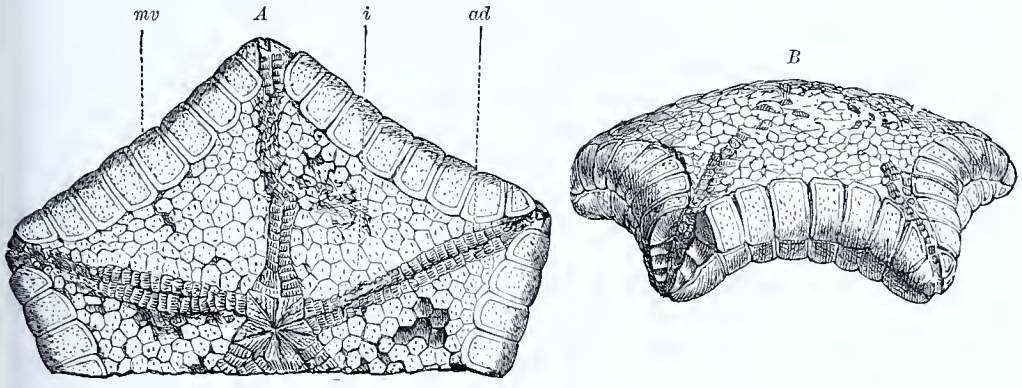

Fig. 340.

Metopaster Parkinsoni, Forbes sp. Lower Chalk; Sussex. *A*, Ventral aspect. *B*, Viewed from one side (after Forbes).

plates of variable size and thickness, which are of not uncommon occurrence in the Jura of Wurtemberg and Switzerland. Some of them bear strong

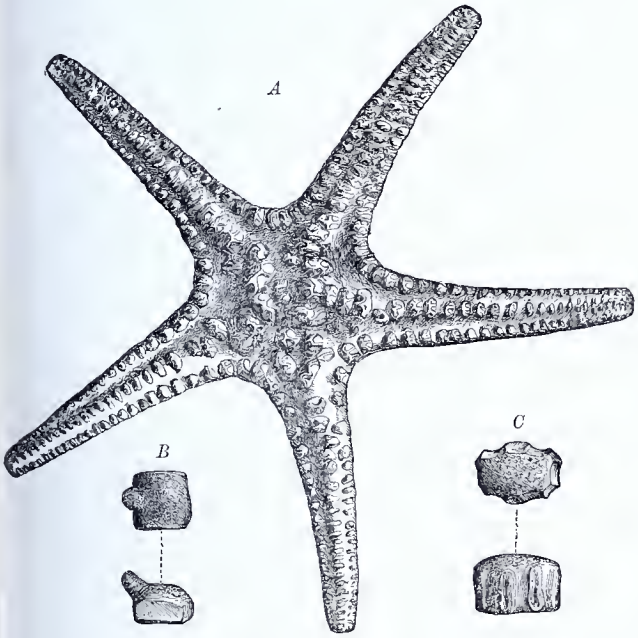

Fig. 341.

A, *Pentaceros jurassicus*, Zitt. Upper Jura; Bemfeld, near Ingolstadt, Bavaria. 1/2. *B*, *P. thoracifer*, Gein. Plänер; Plauen, Saxony. Marginal plate. *C*, *P. primaevus*, Zitt. Upper Jura; Streitberg.

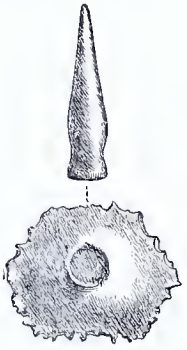

Fig. 342.

Sphaerites scutatus, Goldf. Upper Jura; Sontheim, Wurtemberg.

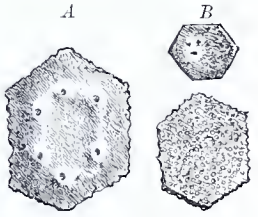

Fig. 343.

A, *Sphaerites tabulatus*, Goldf. *B*, *S. punctatus*, Goldf. Upper Jura; Streitberg, Franconia.

conical spines (Fig. 342), and others are smooth or punctate (Fig. 343). Their zoological position has not as yet been satisfactorily determined.

Order 2. CRYPTOZONIA. Sladen.

Marginal plates inconspicuous and more or less rudimentary in the adult. Supero-marginal plates often separated from the infero-marginal series by intermediate plates. Papulae distributed over the whole body. Ambulacral plates crowded and narrow; tube feet in two or four rows.

Of the Palaeozoic representatives of this order, the genera *Lepidaster*, Forbes (Silurian), and *Roemeraster*, Stürtz (Devonian), are related to the recent genus *Linckia*, Nardo. The forms described by Stürtz, *Echinasterella*, *Medusaster*, and *Protasteracanthion*, from the Devonian of Bundenbach, are regarded by their author as allied to the *Echinasteridae*, *Asteriidae*, and *Brisingidae* respectively.

Solaster, Forbes, is represented by a form having numerous arms in the Great Oolite of England. *Tropidaster*, Forbes, occurs in the Middle Lias; and a solitary species of *Echinaster*, M. and T. (*Rhopia*, Gray), has been described from the Neocomian. A form described by Forbes from the Red Crag of England was considered by him to be specifically identical with the existing *Asterias rubens*, Linné.[1]

Sub-Branch III. **Echinozoa.** Leuckart.

Armless and stemless Echinodermata, with globular, cordiform, discoidal, or worm-like bodies, which are either encased in a plated test or are covered with a leathery skin, in which minute, detached calcareous bodies are embedded.

The *Echinozoa* are divided into two classes: *Echinoidea* or Sea-urchins, and *Holothurioidea* or Sea-cucumbers.

Class 1. ECHINOIDEA. Agassiz. Sea-Urchins.[2]

Echinozoa, with bodies encased in a solid or slightly flexible test, variable in shape from spherical to flat; composed of numerous, closely placed, more or less geometrical

[1] [To Mr. W. Percy Sladen, Vice-President of the Linnean Society, and well known for his numerous scientific achievements, the author and editor are under special obligations for having thoroughly revised and enlarged the preceding chapter on the *Asterozoa*, and also for having rendered valuable assistance on the *Echinozoa*.—Trans.]

[2] *Agassiz, L.*, and *Desor, E.*, Description des Échinides fossiles de la Suisse, 1839-40.—Catalogue Raisonné des Familles, Genres, et des Espèces de la Classe des Échinides (Ann. des. Sci. Nat.), 1846-47.—*d'Orbigny, A.*, Paléontologie française (Terrain crétace, vol. VI.), 1853-60.—*Cotteau* and *Triger*, Échinides du departement de la Sarthe, 1855-69.—*Desor, E.*, Synopsis des Échinides fossiles. Paris, 1858.—*Wright, T.*, Monograph on the British fossil Echinodermata of the Oolitic Formations (Palaeontograph. Soc.), 1857-80.—*Idem*, Cretaceous Formations (Palaeont. Soc.), 1864-82.—*Cotteau, G.*, Paléontologie française, vols. VII., IX., and X., 1862-79.—*Laube, G. C.*, Echinodermen des vicentischen Tertiärgebietes (Denkschr. Wien. Akad. xxix.), 1868.—*de Loriol, P.*, Échinologie helvétique, vols. I.-III. Geneva, 1868-75.—*Quenstedt, F. A.*, Petrefactenkunde Deutschlands (Bd. III., Echiniden), 1872-75.—*Agassiz, A.*, Revision of the Echini (Ill. Cat. Museum Comp. Zool. Cambridge, No. 7), 1872-74.—Reports on the Echini of the Hassler (1874), Challenger (1881) and Blake (1883) Expeditions.—*Lovén, S.*, Études sur les Échinoïdées (Svensk. Vetensk. Akad. Handl., Bd. XI.), 1874.—*Cotteau, Peron*, and *Gauthier*, Échinides fossiles de l'Algérie. Paris, 1876-91.—*de Loriol, P.*, Monographie paléontologique, etc. (Abhandl. Schweiz. pal. Gesellsch. III.-VIII.), 1876-81.—*Dames, W.*, Die Echiniden der vicentischen und veronischen Tertiär-Ablagerungen (Palaeontographica, Bd. XXV.), 1877.—*Agassiz, A.*, Palaeontological and Embryological Development (Address before Amer. Assoc. Adv. Science), 1880.—Bibliography of the Echinodermata (Bull. Museum Comp. Zool. Cambridge, vol. X., No. 2), 1882.—*Duncan, P. M.*, and *Sladen, W. P.*, Monograph of the fossil Echinoidea of Western Sind (Palaeont. Indica, Ser.

plates, covered with soft structures, and carrying spines. Mouth on the under or actinal surface; anus situated either in the dorso-central system or somewhere in the posterior interambulacrum. Plates of the five ambulacral areas more or less extensively perforated for the protrusion of tube feet.

The Test.—The test or covering of Echinoids is composed of numerous calcareous plates, firmly united by their edges, so as to form a more or less rigid case or box, and disposed in certain regions or systems. In a few instances, however, the plates overlap one another in an imbricating manner, so as to impart a certain degree of flexibility to the test. The main element of the test is called the *corona*, and the system of plates at the summit is known as the *dorso-central* or *apical system.*

The test is pierced by two large openings, which are surrounded by membranes studded with small calcareous particles. One of these is the *mouth*, which is always placed on the under or actinal surface of the body, may be either central or eccentric in position, and is surrounded by a coriaceous peristomial membrane. The other aperture is the *anus*, surrounded by a periproctal membrane. In some orders it is placed opposite the mouth in the centre of the apical system, in which case the test is said to be *regular* or *endocyclic.* But in other orders it is situated beyond the apical system at a variable distance in the median line of the posterior interambulacrum, either dorsally or actinally; the test is then said to be *irregular* or *exocyclic.*

The mouth opens into an oesophagus, which conducts into a capacious stomach, and thence into a convoluted intestine. The digestive tract winds round the interior of the test, being attached to the inner surface of the latter by muscles, and terminates in the anus. Surrounding the oesophagus is a circular vessel filled with water, which is admitted by the so-called *stone canal*, opening externally in a *madreporite.* This is a porous or sieve-like structure, consisting of a variable number of canals, and though commonly restricted to one of the plates of the apical system, it may extend backwards and perforate a large part of the system.

The circular vessel gives off five branches, known as the *radiating canals*, which pass along the ambulacral areas on the interior of the test, and connected with it in the interambulacral areas are five distensible membranous reservoirs, termed the *Polian vesicles.* The radiating canals give off numerous lateral branches or *tube feet* (*tentacles*, *pedicels*) which are capable of protrusion through pores of the ambulacral plates. Emission is effected by means of secondary vesicles or *ampullae* which by contraction force their contained fluid into the tube feet and distend them. The ampullae, as a rule, communicate with the tube feet by two canals perforating the plates separately, a single tentacle being placed over a pair of ambulacral pores. The tube feet serve normally as locomotive organs, when they are prehensile and end in a suctorial disk; but in many forms, especially those having petaloid ambulacra, they are

XIV.), 1882-84.—*Schlüter, C.*, Die regulären Echiniden der norddeutschen Kreide (Abhandl. zur geolog. Special-Karte von Preussen, Bd. IV.), 1883.—*Idem*, Neue Folge, Heft 5, 1892.—*de Loriol, P.*, Description des Échinides (Commission des travaux géol. du Portugal, vol. II.), 1887-88.—*Lovén, S.*, On Pourtalesia (Svensk. Vetensk. Akad. Handl., Bd. XIX.), 1884.—*Pomel, N. A.*, Classification méthodique et genera des Échinides vivantes et fossiles, 1883.—*Duncan, P. M.*, Revision of the Genera and Great Groups of the Echinoidea (Journ. Linn. Soc., vol. XXIII.), 1889.—*Ebert, T.*, Die Echiniden des nord- und mittel-deutschen Oligocäns (Abhandl. zur geol. Spec. Karte von Preussen, Bd. X.), 1889.—*Lovén, S.*, Echinologica (Bihang till Svensk. Vetensk. Akad. Handl., Bd. XVIII.), 1892.—*Clark, W. B.*, Mesozoic Echinodermata of the United States (Bull. U.S. Geol. Survey, No. 97), 1893.

modified so as to be partly branchial in function. Sometimes the tentacles of the same ambulacrum differ in shape, structure, and function, in which case they are termed *heteropodous*. Small tufts of external branchiae communicating with the ambulacral system are sometimes present, and occupy grooves or incisions in the peristomial margin.

The *vascular system* consists of a ring-like vascular plexus surrounding the oesophagus, and immediately underlying the circular ambulacral vessel. This ring gives off five radial vessels, and also two others which send off branches to the stomach and generative organs. The central *nerve ring*, with its five principal nerves running down the rays, is external to the two other systems. The *generative organs* are extremely alike in both sexes, and are in the form of glands (usually five, sometimes three or even two), situated dorsally and interradially on the inner surface of the test. The genital ducts terminate in pores in the so-called genital plates, to be described presently.

Coronal Plates.—The plates of the corona are arranged in ten meridional zones. Five of these, the *ambulacral areas*, are composed of perforated plates, and correspond in position to the radiating ambulacral vessels; the remaining five, the *interambulacral* or *interradial areas*, alternate with the first, and are imperforate.

In all recent, and in the majority of fossil Echinoids, the ambulacral areas are composed of two rows of small, alternately arranged plates, the inner edges of which meet in zigzag median sutures, and their actinal and abactinal edges in horizontal sutures. The interambulacral areas are likewise composed of two rows of plates, but they are generally larger than those of the ambulacra, and meet them in ambulacro-interradial vertical sutures. There are normally, therefore, twenty meridional rows of plates arranged in ten alternating zones; but this number is not fully attained in the Palaeozoic *Bothrioeidaroida*, and is exceeded in the remainder of the *Palæechinoidea*, in the Triassic *Tiaraechinus*, and in the Cretaceous *Tetracidaris*. The number of plates is the same in all of the ambulacral and all of the interambulacral areas respectively; but the two systems are entirely independent of one another as respects the size, shape, and number of the plates. In the *Cidaridae*, for example, the ambulacra are very narrow, and are composed of from fifty to sixty plates in each column; the interambulacra are much broader, and consist of four or five large plates in each column. In the regular Sea-urchins, or *Endocyclica*, all of the ambulacra and all of the interambulacra are similar; but in the *Exocyclica*, the anterior ambulacrum and the posterior interambulacrum often differ considerably from the corresponding areas.

Interambulacral (interradial) plates are always simple; ambulacral plates may be either simple or compound. In the latter case, they may be formed of two or of several components, all of which are joined by sutures and form a more or less geometrical plate. Most simple plates, and some of the components are *primaries*—that is, they extend from the outer edge of an ambulacrum to the median suture of the area. *Demi-plates* is a name applied to those components which do not reach the median line.

The growth of the test in all Echinoids is effected by new plates being successively added at the aboral termination of the ambulacra and interambulacra, and by their increasing in size and solidity. In the young condition generally, and in the Clypeastroids and Spatangoids throughout life, the interambulacra begin ventrally with a single plate, situated outside the

closed circle formed by the double column of paired ambulacral plates; and this solitary interambulacral plate is followed by a double column of successively added plates, the last-formed being contiguous with the corresponding basal of the apical system. But in the *Endocyclica*, according to Lovén, the primordial interambulacral plate is soon resorbed, so that the interambulacra enter the peristomial margin with two plates each.

Ambulacra.—Each ambulacrum consists of an interporiferous area, placed between two poriferous zones; only a few Palaeozoic genera have the whole ambulacral area poriferous. As a rule, the ambulacral pores are in pairs; but in some cases they are unpaired. The pores may be either all similar, or the outer pores of a series of pairs may differ in shape and size from those of the inner series. There is usually a septum between the pores of a pair, and the pairs may be separated by costae. When the pores of each pair are united by transverse furrows, they are said to be *conjugate*.

The arrangement of the pairs of pores may be in *simple series*, when one pair is placed over the other from peristome to apex; they are *biserial* ("bigeminal" auct.) when placed so that there are two vertical rows of pairs, one nearer the ambulacro-interradial suture than the other; and *triserial* ("trigeminal") when there are three vertical rows of pairs. Simple series of pores are either absolutely straight, or in *arcs* of three or more pairs. Oblique series are those in which there is an outward slant of three or more consecutive pairs from above downwards.

Ambulacra are *simple* or *perfect* when they are band-shaped and continuous from pole to pole, or when the direction of the pairs of pores is but slightly flexuous. *Petaloid* or *circumscript* ambulacra are those which enlarge between the apex and equatorial circumference (*ambitus*), and contract again more or less perfectly before reaching that region. *Sub-petaloid* ambulacra are more elongated than the petaloid, and the pairs of pores do not tend to close distally. The pores do not cease altogether at the end of the petaloid parts, but remain traceable for some distance beyond, often as far as the mouth. In such cases, however, the rows become uniserial, and the pores are greatly reduced in size, or present other marked differences from those of the petaloid parts. The poriferous zones are said to be *discontinuous* or *interrupted* when the pairs of pores cease at the ends of the petals, and reappear in the vicinity of the mouth. Sometimes the dorsal portions of the ambulacra are petaloid, and the rest simple, except often near the peristome.

Dorso-central or *Apical System.*—This is abactinal or dorsal, and is ordinarily composed of ten plates arranged in two alternating zones or circles of five plates each. The uppermost circle is interradially situated, and consists of large pentagonal or hexagonal pieces, called the *basal* or *genital plates*. These are usually perforated by one or more ducts communicating with the genital glands; but when less than the full number of glands are developed, the corresponding basal plates are impunctate. The posterior basal is very often imperfectly developed or absent. The lower circle of plates occupies the summit of the ambulacra, and consists of five smaller *radial plates* (formerly termed "ocular plates"), which are also perforated. In the *Palæechinoidea* the radial plates may be pierced by more than one canal; but all other Echinoids have but a single canal to each radial, terminating in a single or double orifice. These openings appear to relate to a primitive large tentacle, and not to an ocular organ.

One of the basal plates, namely, the right anterior one, is generally larger than the rest, and serves at the same time as the madreporic body. This fact greatly facilitates the orientation, whenever the madreporite is preserved; unfortunately, however, it is indistinguishable in the majority of fossil specimens. The anterior radial plate is that lying to the front and on the left hand of the madreporite-bearing basal; and it surmounts the odd or anterior ambulacrum (Fig. 344, *D*). It is evident from the inspection of any Sea-

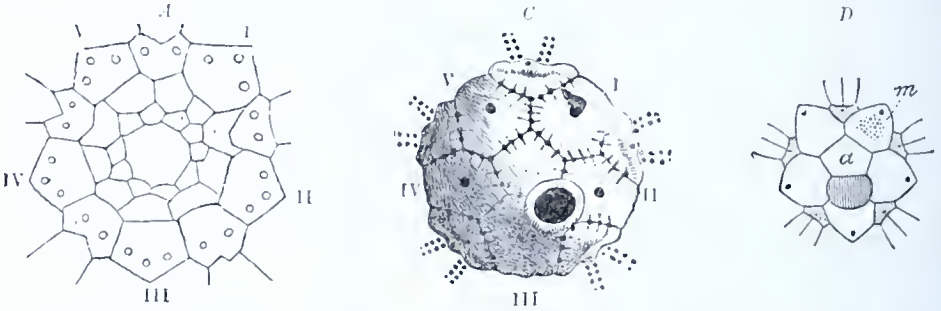

Fig. 344.

Apical systems of *A*, *Palæechinus*. *C*, *Salenia*. *D*, *Peltastes*, enlarged. The *Amb* are designated I—V.

urchin that a plane passing through the odd ambulacrum, mouth, anus, and the posterior interambulacrum, will divide the test into two symmetrical halves.

In the *Exocyclica* the basal plates may be in contact at their sides, forming a *compact system* (Fig. 345, *B*, *D*); or they may be separated by some of the radial plates which unite along the median line and push the posterior basals backward, forming an *elongate system* (Fig. 345, *C*). When the two posterior ambulacra (*bivium*) do not terminate at the summit in line with the other three (*trivium*), and are surmounted by radials placed far posteriorly, the system is said to be *disjunct* or *disconnected*. The posterior radials are then separated from the postero-lateral basals by a number of interambulacral plates intercalated along the dorsum (Fig. 345, *A*).

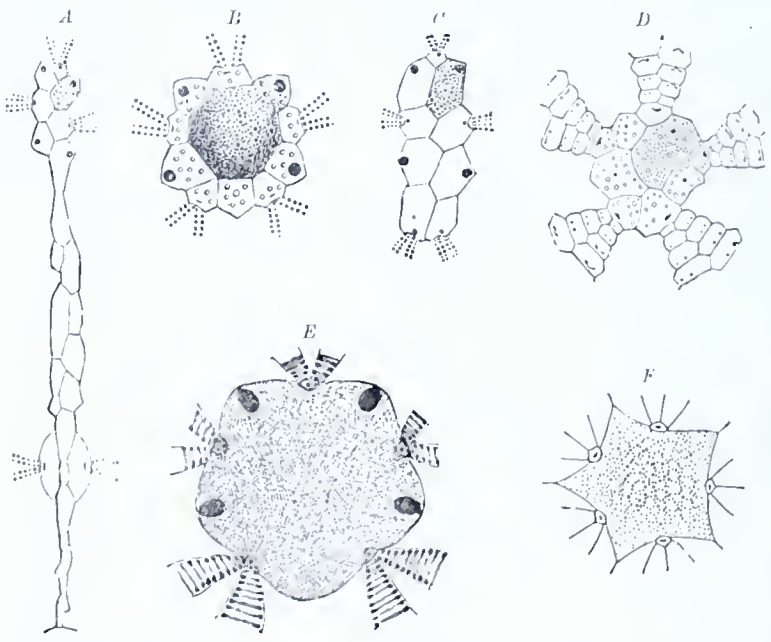

Fig. 345.

Apical systems of irregular Sea-urchins. *A*, *Collyrites*. *B*, *Holectypus*. *C*, *Hybo-clypus*. *D*, *Micraster*. *E*, *Conoclypeus*. *F*, *Clypeaster*.

In the *Clypeastridae*, *Holectypoida*, and many of the *Cassidulidae*, the apical system consists of five minute radial plates, and one large, pentagonal, central

plate, which probably represents five fused basals, and is usually pierced in four or in all of its interradial angles by genital pores (Fig. 345, *E*, *F*).

Periproct.—This is within the apical system in all regular Sea-urchins, and at a variable distance beyond it in the median line of the posterior interambulacrum when the test is exocyclic. The plates of the periproctal membrane may be few and symmetrical, or numerous and irregular, and arranged concentrically about the anal orifice. The *Saleniidae* have a large *suranal* plate immediately in front of the latter. The periproct is usually circular, but may vary from elliptical to pyriform. Its position on the test is of great systematic importance.

Peristome.—This is more or less central and actinal in the *Endocyclica*, and is decagonal or pentagonal in contour; and there are not infrequently five or ten incisions along its edges for the reception of external branchiae. In the *Exocyclica* it is variable in shape and position, but is usually actinal, and eccentric in front. Sometimes it is semilunar in outline, with a posterior

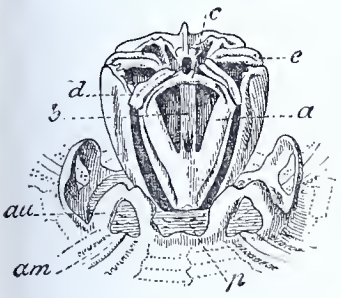

FIG. 346

Dental system of the recent *Echinus miliaris*, Leske, seen from within the test. *a*, Jaws or pyramids; *b*, Tooth; *c*, Epiphysis or arcus; *d*, Brace; *e*, Rotula or compass; *p*, Peristome; *am*, Ambulacrum; *au*, Auricles (after Bertrand).

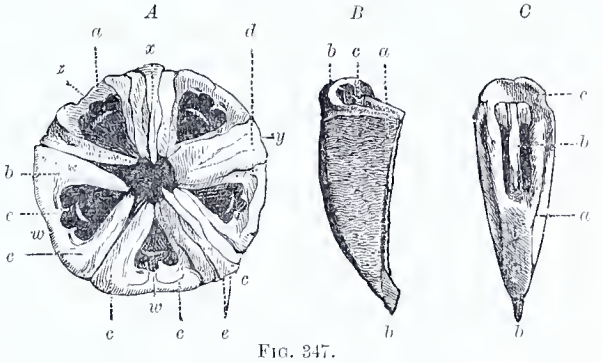

FIG. 347.

Dental apparatus of *Sphaerechinus*. *A*, View of the flat upper surface. *a*, Half-pyramid with overlying pieces removed; *b*, *c*, Epiphyses; *d*, Brace (*Zwischenkieferstück*); *e*, *x*, Rotulae or compasses; *w*, Symphyses of the half-pyramids, with alveoli on the inner face. The letters *y* and *z* mark the *Amb* and *IAmb* areas, respectively. *B*, *C*, Half-pyramids seen sidewise and from within. *a*, Lateral wings; *b*, Tooth; *c*, Supra-alveolar process.

labrum. Its plated membrane is attached to the pyramids of the jaws in Gnathostomes; otherwise the inner edge is free.

Around the peristome the pairs of ambulacral pores are often *crowded*. Or they may form a kind of rosette, in which some of the pairs are wider apart than others, and some are put out of place and doubled; such an arrangement is called a *phyllode*. In the *Cassidulidae* the phyllodes are sunken, and the interambulacral areas between them are swollen so as to form lip-shaped ridges (*bourrelets buccaux*), the whole forming a *floscelle* about the mouth.

Jaws.—All Sea-urchins, with the exception of the Spatangoids, and possibly some of the Holectypoids, are provided with a powerful masticatory apparatus, commonly known as "Aristotle's Lantern." In the *Endocyclica* (Figs. 346, 347) the system consists of five hard interradially situated teeth, which are in relation with as many *pyramids* resting upon the peristome internally, and whose free ends are capable of being moved towards one another or apart. The pyramids form collectively a hollow cone or three-sided pyramid, with the apex directed downwards, and the teeth slightly projecting beyond the peristome. The pyramids are connected with one another by muscles at their sides; at their upper junction there are five

braces (*falces, Zwischenkieferstücke*) radiating outwards from the central axis of the jaws; and above each brace there is a long bifid process, the *rotula* or *compass* (*Gabelstück*). Each pyramid has an outer concave face, and two flattened sides, forming a hollow groove in which the tooth runs. The teeth are correspondingly grooved or keeled, pointed actinally, and are more or less vertical.

The jaws of the exocyclic Gnathostomes are similar to those just described, except in the Clypeastroids, where they are low, often unsymmetrical, and the teeth are aslant or even nearly horizontal (Fig. 348). Rotulae are absent, and the braces are rudimentary. The pyramids are solid almost to their upper part, more or less concave, or re-entering on the outer side, and are not always of the same size. Jaws are rarely preserved in the fossil state.

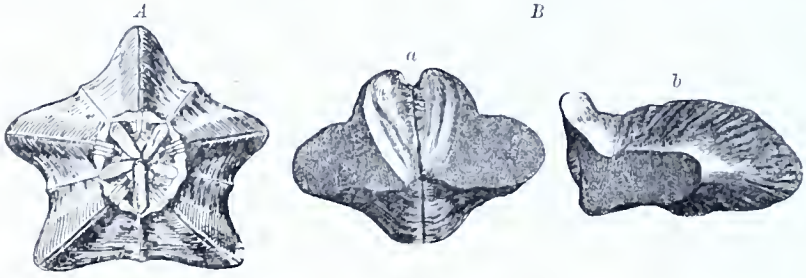

FIG. 348.

A, Clypeaster reticulatus, Lovén. Recent. The dental system entire, seen from above. The rotulae are placed upon the sutures of adjoining pyramids, with an epiphysis on either side. Teeth in line with the mesial sutures of half-pyramids, and within the ring formed by the supra-alveolar crests (after Lovén). *B, a*, Front view of a single pyramid. *B, b*, Side view of one of the half-pyramids.

All Echinoids having a dental system are provided also with a *perignathic girdle* (also termed *auricles*). This is a structure composed of ambulacral processes and interambulacral ridges, which together surround and underlie the jaws, and furnish attachment for their muscles. The girdle is *continuous* when the ambulacral processes are arched over and connected at their sides by ridges consisting of turned up and fused interambulacral plates; and *discontinuous*, as in *Cidaris* and the Clypeastroids, when there are either simple ridges or simple processes without their union (Duncan). The girdle is developed from the test itself, and does not therefore belong to the dental system.

Tubercles and Spines.—The plates of Echinoids are almost always covered with wart-like tubercles and granules, which carry various kinds and sizes of spines. The larger and completely developed tubercles are called *primaries;* those of a smaller size are *secondaries;* and very small tubercles, sometimes incomplete in their development, are *miliaries*. *Granules* are irregular or nodular projections of the test; they may be large and widely separated, or very numerous and of various sizes. The base of a tubercle is termed the *boss*, and its upper part may be either plain or crenulated. The boss supports a rounded *mamelon*, which is said to be *perforated* when pierced by a central foramen for a slight distance, or *imperforate* when it is not. A plain or sunken space surrounding the base of the tubercle is called the *scrobicule*, or *areole;* its outer limit, the *scrobicular circle*, is generally marked by a ring of granules, but in many cases the scrobicules of the same meridian are continuous. Secondary tubercles may or may not be scrobiculate.

All the tubercles of Sea-urchins bear movable *spines*, which vary greatly in dimensions, and in the shape and nature of their cross-sections. They are

usually cylindrical, acicular, clavate, or spatulate in form, and consist of the following parts :—A more or less elongate distal portion or *shaft;* a *base*, to which ligaments are attached for keeping the spine in place; and an articulating joint or *condyle* (*acetabulum*), forming a ball and socket joint with the tubercle proper. When the base of the mamelon is crenulated, the base of the spine is incised in the same manner, and above the latter is usually a milled ring or *collar*, the indentations of which are continuous with the striæ of the shaft. The function of spines is to support the test, to aid in locomotion, and for defence. In rare cases some of the spines are fixed, and arise directly from the test (*Podocidaris*).

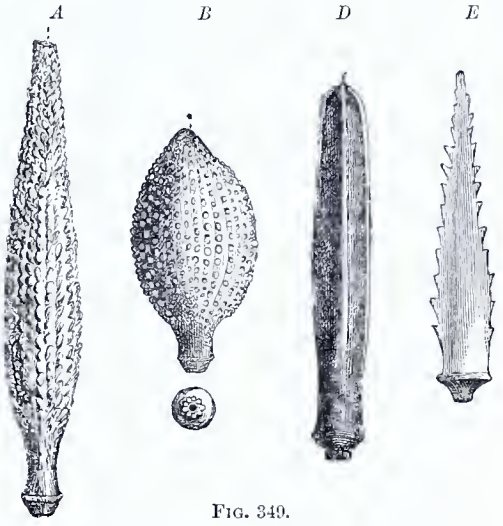

Fig. 349.

Cidarid Spines. *A, B, Cidaris. D, Acrocidaris. E, Porocidaris.*

Fascioles are narrow bands of close granular ornamentation which support rudimentary spinules and pedicellariae. They occur only in the Spatangoids, and are restricted to certain parts of the test. The *peripetalous* fasciole follows the margin of the petaloid parts of the ambulacra. The *anal* fasciole surrounds the anus, and the *subanal* fasciole encloses a space or *plastron* beneath the anus, but may send anal branches upward. The *internal* fasciole crosses the ambulacra at a variable distance from the apical system, and the *marginal* fasciole encircles the test above the ambitus. For those Spatangoids with subanal fascioles, Lovén has proposed the name *Prymnodesmia;* genera without them, and with other fascioles, are *Prymnadetes*, and those without any fascioles are *Adetes*.

Pedicellariae are small, highly specialised spines articulated upon granules, and scattered in between the spines proper over the whole surface of the test. At the end of the stem is a head consisting of two or three pincer-like valves, whose office is to catch up and pass along foreign matter that has become entangled among the tubercles and spines.

Spheridia are opalescent spheroidal bodies which are either placed visibly upon short stalks, or are partially or even entirely covered by the test. They occur in all Echinoids with the exception of the *Cidaridae*, belong exclusively to the ambulacra, and are found usually near the peristome. Anatomically the spheridia may be considered as modified spines having sensory functions, probably of taste or of smelling.

Ontogeny.—The early ontogenetic stages of Sea-urchins are similar in many respects to those of Ophiuroids and Star-fishes, but have little in common with the larvae of Crinoids. Certain changes affecting the test during the course of its development are of great morphological interest, such as the formation of tubercles, variations in the number of plates in the *Echinidae* and other of the *Regulares*, the transformation of simple ambulacra into petaloid in the *Echinolampidae;* the migratory character of the periproct in many Cassiduloids, etc. Much light is shed upon these phenomena by comparison with fossil forms, many of which retain permanently features which are now exhibited transitorily.

Homologies.—The *Echinoidea* differ radically from the *Pelmatozoa* and *Asterozoa* in that arms are completely wanting; and although the principal viscera (ambulacral, blood, nervous, and digestive systems) are similarly formed and situated, the dermal skeleton, on the other hand, is very differently developed in the three groups. The ambulacra of Echinoids are without arm supports, vertebral disks, or ambulacral ossicles. The system is confined to the interior of the test, and is covered over with plates which are possibly comparable with the adambulacral plates of the *Pelmatozoa* and *Asteroidea*. Great phyletic importance was attached by A. Agassiz, Lovén, and P. H. Carpenter to the homology between the dorso-central system of Sea-urchins and the base of Pelmatozoans; the basals and radials of that system being supposed to correspond to the like-named plates of Crinoids; and the large central plate developed in the periproct of young *Regulares* (the so-called dorso-central plate) was regarded by Lovén and others as the solidified homologue of five crinoid basals or under-basals, whilst Carpenter considered it to be the equivalent of the radical plate or root-disk at the extremity of the Crinoid stem. Neumayr, Semon, and others have, however, advanced weighty arguments against this hypothesis, and regard all of the above-mentioned resemblances as cases of parallelism.[1]

Habits.—Sea-urchins are exclusively marine forms, and all are more or less gregarious. Many species abound in littoral zones, some thriving on the edge of low-water mark (*Clypeastridae*). Others are found in zones ranging from 400-600 fathoms (*Diadematoidea*), and a few have been dredged from a depth of nearly 3000 fathoms. Numerous endocyclic Sea-urchins, along coasts exposed to the action of the waves, live in cavities which they bore with their teeth out of the solid rocks. The same species, however, does not excavate in sheltered places.

About 300 recent species are known, as compared with fully 2500 fossil. The earliest types make their appearance in Ordovician rocks (*Bothriocidaris*), and continue to be represented sparsely throughout the Palaeozoic era. They multiply enormously in the Mesozoic, and reach the climax of their development in the early Tertiary; after which they begin steadily to decline. As a rule, the species have a very limited vertical range, and hence serve admirably as index fossils. The test is often perfectly preserved, but even small fragments are capable of accurate determination, owing to the regular repetition of isomeres.

The number of meridional rows of plates in the corona is used as a basis for dividing the *Echinoidea* into two sub-classes—*Palæechinoidea* and *Euechinoidea*.

Sub-Class 1. PALÆECHINOIDEA. Zittel.

Test composed of more than twenty meridional rows of plates, or in one order (Bothriocidaroida) of less than twenty. Plates of the areas overlapping or not. Peristome actinal, central, with jaws. Periproct within the dorso-central system or in the posterior interambulacrum beyond (Cystocidaroida).

With the exception of the Triassic *Tiarechinus*, all members of this sub-class are restricted to the Palaeozoic era.

[1] [For valuable notes on the homologies of Echinoderms, see *Agassiz, A.*, Calamocrinus Diomedae (Mem. Museum Comp. Zool. Cambridge, vol. XVII, pp. 84-96), 1892.—Trans.]

Order 1. CYSTOCIDAROIDA. Zittel.

Test exocyclic, globular or ovoid, thin. Ambulacra narrow, straight, with four vertical rows of plates, each with a central pair of pores. Interambulacra broad, with numerous vertical rows of irregular, scale-like plates, each with a small primary tubercle surrounded by a scrobicule. Periproct in the posterior interambulacrum above the ambitus. Peristome small, with highly-developed jaws.

Echinocystites, Wyv. Thoms. (*Cystocidaris*, Zitt.) This aberrant genus, with the characters of the order, occurs in the Silurian of Scotland, and was regarded by its founder as transitional between the *Echinoidea* and *Cystoidea*.

Order 2. BOTHRIOCIDAROIDA. Zittel.

Test regular, more or less spherical. Interambulacra with one, and ambulacra with two vertical rows of plates, which do not imbricate. Periproct in the apical system.

The solitary genus is *Bothriocidaris*, Eichwald (Fig. 350), from the Ordo-

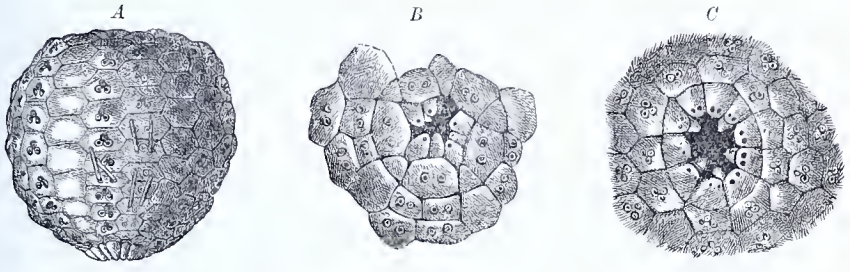

Fig. 350.

Bothriocidaris Pahleni, Schmidt. Ordovician; Nõmmis, Esthonia. *A*, Test of the natural size. *B*, Apical system, enlarged. *C*, Peristome, enlarged (after F. Schmidt).

vician of Esthonia. The test is small, and the apical system consists of five large radial plates limiting the periproct, each with two pores; and five small imperforate basal plates.

Order 3. PERISCHOËCHINOIDA. M'Coy.

Test regular, globular or ovoid, with more than two vertical rows of interambulacral plates; and with two or many columns of ambulacral plates, each with a pair of pores. Plates thick and rigid, or thinner and more or less overlapping.

Family 1. Archaeocidaridae. M'Coy.

Ambulacra narrow, each with only two columns of poriferous plates. Interambulacral plates with bevelled edges, and usually overlapping. Devonian to Permian.

Lepidocentrus, Müller (Fig. 351). *Amb* with five to eleven columns of plates at the ambitus. *Amb* very narrow, with low broad plates, and continued beyond the peristomial margin to the true mouth. Tubercles distant; spines small, subulate. Devonian; Europe.

Koninckocidaris, Dollo and Buiss. Europe. *Perischodomus*, M'Coy. Carboniferous; Europe and North America.

Archaeocidaris, M'Coy (*Palaeocidaris*, Desor), (Fig. 352). Test large. *Amb* straight, reaching to the stoma; plates irregular, imbricating adorally. *IAmb*

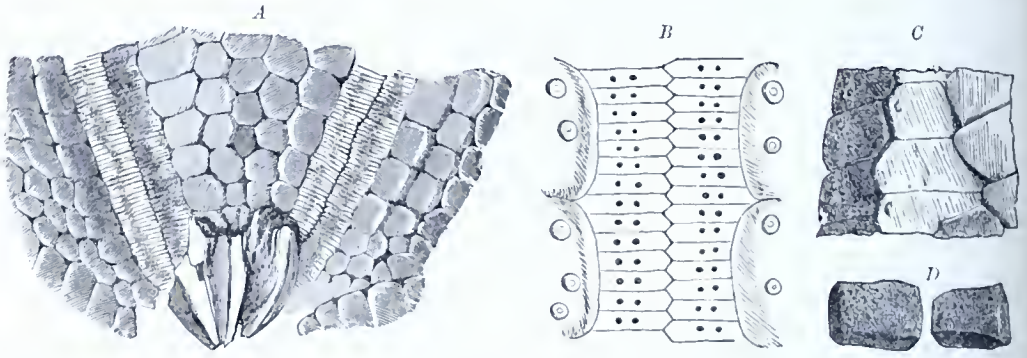

Fig. 351.

A, *Lepidocentrus Rhenanus*, Beyr. Devonian; Wipperfürth, Eifel. Cast of the interior of test showing jaws, $^1/_1$ (after J. Müller). *B-D*, *Lepidocentrus Mülleri*, Schultze. Devonian; Gerolstein, Eifel. *B*, Portion of *Amb*, enlarged. *C*, Several *IAmb* plates, $^1/_1$. *D*, Two detached *IAmb* plates, showing oblique edges, $^1/_1$.

with three to seven columns of large thin plates, the median ones hexagonal, the adambulacral pentagonal or rounded. Median plates bevelled slightly over those on either side, and these over others to the ambulacral edge. Each *IAmb*

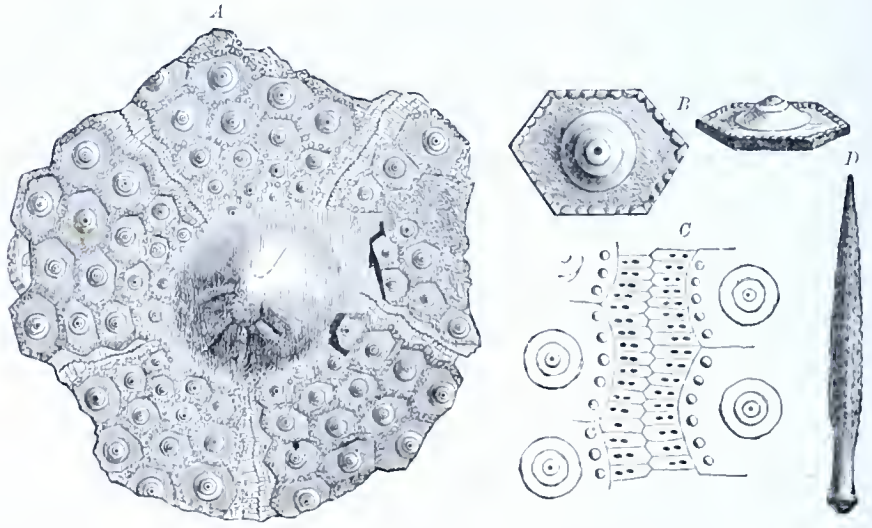

Fig. 352.

Archaeocidaris Wortheni, Hall. Sub-Carboniferous; Burlington, Iowa. *A*, Portion of ventral region, showing jaws, $^1/_1$. *B*, An *IAmb* plate viewed from above and from the side. *C*, Portion of *Amb*, enlarged. *D*, Spine, $^1/_1$ (after Hall).

plate with a large primary tubercle, surrounded by a large flat scrobicule and a circlet of granules. Primary spines large, usually serrated. Carboniferous Limestone; Great Britain and North America. Permian; England.

Lepidocidaris, Meek and Worthen. Sub-Carboniferous; North America. *Lepidechinus*, Hall. Upper Devonian and Sub-Carboniferous; North America.

Xenocidaris, Schultze. Founded upon clavate spines from the Devonian of the Eifel.

Family 2. **Melonitidae.** Zittel.[1]

Ambulacra more or less broad, composed of several columns of poriferous plates in all genera except Palæechinus and Rhoëchinus, where there are but two. Carboniferous.

Palæechinus (Scouler), M'Coy (Fig. 353). Test spheroidal, rigid. *Amb* straight, composed of two vertical rows of low thick plates, extending across the half *Amb* or not. Pairs of pores in two vertical rows on each side of an *Amb;* the outer pairs either in demi-plates or primaries; the inner pairs always in primaries, which may, however, be short. *IAmb* broad, convex, with five to eight columns of tumid plates, diminishing toward the poles. Periproct in apical system, surrounded by five large basal plates, each perforated by one or three canals, and five doubly perforated radial plates. Silurian; England. Carboniferous Limestone; Great Britain.

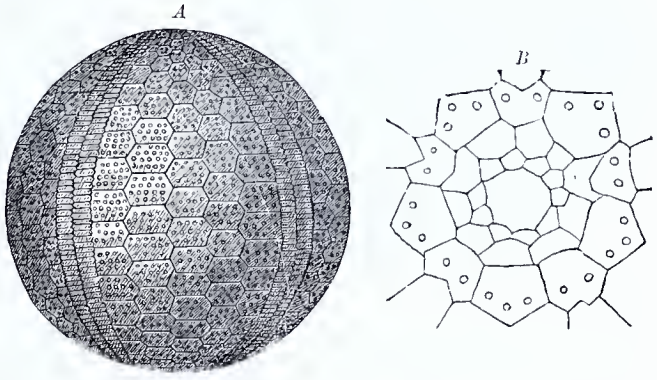

Fig. 353.

Palæechinus elegans, M'Coy. Carboniferous Limestone; Ireland. *A*, Test, 1/1. *B*, Apical system, enlarged (after Baily).

Rhoëchinus, Keeping. Like the preceding, but ambulacral plates never compound, and only one vertical row of pore pairs on each side of an *Amb*, a pair to each plate. *IAmb* with four to eight columns of plates diminishing toward the poles, slightly overlapping. Radials sometimes wanting. Carboniferous Limestone; Great Britain. Sub-Carboniferous; North America.

Oligoporus, Meek and Worthen. Like *Melonites*, but *Amb* with only four columns of plates, and *IAmb* with five to nine columns at the ambitus, diminishing in number toward the poles. According to Jackson, the interambulacral plates develop like those of *Melonites*. The *Amb* terminate at the peristomial margin in two plates, which pass gradually by lateral expansion into the four columns of the adult. Sub-Carboniferous; North America.

Melonites, Norwood and Owen (Fig. 354). Test very large, ellipsoidal, grooved longitudinally. *Amb* broad, concave on both sides of a median ridge, with six to twelve columns of plates, each perforated near its outer border by a pair of pores. Plates slightly imbricated, the median rows the largest. *IAmb* with four to eleven columns of plates, diminishing in number toward the poles. The median plates are hexagonal; the two rows adjacent to the *Amb* pentagonal, with the edges indented by the zigzag of the ambulacro-interradial suture. Edges of plates sometimes oblique, especially when thick. Tubercles very

[1] *Roemer, F.*, Ueber den Bau von Melonites multipora (Arch. für Naturgesch. Bd. XXI.), 1855.
Etheridge, R., On Relationships between the Echinothuridae and Perischoechinidae (Quar. Journ. Geol. Soc. vol. XXX.), 1874.
Keeping, W., On the Discovery of Melonites in Britain (Quar. Journ. Geol. Soc. vol. XXXII.), 1876.
Duncan, P. M., On the Anatomy of Palæechinus (Ann. and Mag. Nat. Hist. [6] vol. III.), 1889.
Keyes, C. R., Palaeozoic Echinodermata (Proc. Iowa Acad. Sci. vol. II.), 1894.
Jackson, R. T., and *Jaggar, T. A.*, Studies of Melonites multiporus (Bull. Geol. Soc. America, VII.), 1896.
Jackson, R. T., Studies of Palæechinoidea (Bull. Geol. Soc. America, VII.), 1896.

small, numerous; spines minute, acicular. Periproct circular; basal plates

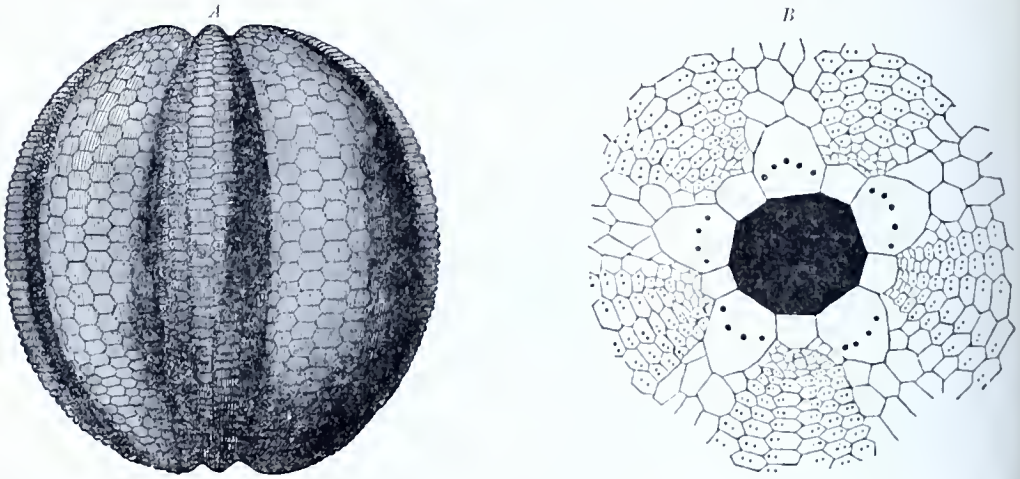

Fig. 354.

Melonites multipora, Norwood and Owen. Sub-Carboniferous; St. Louis, Missouri. *A*, Test, 1/2 natural size. *B*, Dorso-central system, slightly enlarged (after Meek and Worthen).

with three to five genital perforations; radials sometimes with a single pore. Sub-Carboniferous; North America and Europe.

[As shown by Jackson and Jaggar (*Studies of Melonitidae*), the *IAmb* of *Melonites* enter the peristomial margin as two plates. Passing dorsally, new columns are introduced, rapidly at first, until the full complement is reached at or a little above the ambitus. The initial plates of new columns are pentagonal, with a more prominent apex of the pentagon pointing ventrally; and an adjacent plate is characteristically heptagonal, thus facilitating the orientation of obscure fragments. Newly added plates near the dorsal area are more or less rhombic in outline. The *Amb* terminate actinally in four plates; and new vertical columns are added between the median and lateral columns on either side, increasing dorsally.]

Lepidesthes, Meek and Worth. Test large. *Amb* broad, with eight to eighteen columns of small plates imbricating adorally; and pores in single, or occasionally in double pairs. *IAmb* with three or more columns of plates imbricating aborally and laterally. Sub-Carboniferous; North America.

Hyboechinus, Worthen and Miller; *Pholidocidaris*, Meek and Worthen. Sub-Carboniferous; North America.

Family 3. Tiarechinidae. Zittel.

Ambulacra narrow, with two vertical rows of plates pierced by a pair of pores. Interambulacra with a single peristomial plate, followed by three vertically elongated plates only, one on either side of the narrower median plate. Basals large, with two genital perforations; radials smaller, imperforate, and notching the union of the basals slightly.

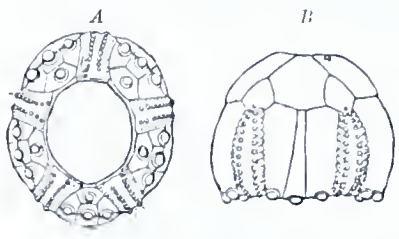

Fig. 355.

Tiarechinus princeps, Laube. Upper Trias; St. Cassian, Tyrol. Ventral and lateral aspects, highly magnified (after Lovén).

Tiarechinus, Neumayr (Fig. 355). The test of this unique genus is very small, flat actinally, and sub-hemispherical dorsally. Below the ambitus and actinally the ornament consists of a plain primary tubercle to each plate; elsewhere the test is coarsely granular, including the very large apical system. The solitary species, *T. princeps*, Laube sp., occurs in the Trias of St. Cassian, Tyrol.

Sub-Class II. EUECHINOIDEA. Bronn.

Test composed of two vertical rows of plates in all of the ambulacra and interambulacra. Periproct either within the dorso-central system or in the posterior interambulacrum at a variable distance beyond. Peristome actinal, rarely anterior. Jaws present or absent. Permian to Recent.

The older division into the two orders of Desor, *Regulares* and *Irregulares* (=*Endocyclica* and *Exocyclica*, Wright), with their further division into two sub-orders each (*Holostomata* and *Glyphostomata* of the endocyclic, and *Gnathostomata* and *Atelostomata* of the exocyclic orders), is now superseded by the erection of five independent orders, as follows:—*Cidaroida, Diadematoida, Holectypoida, Clypeastroida,* and *Spatangoida.* Of these the first two correspond to the *Regulares,* and the remainder to the *Irregulares.*[1]

Order 1. CIDAROIDA. Duncan.

"*Euechinoidea with an actinal, central peristome and an abactinal periproct, situated within the dorso-central system; with internal branchiae only, and having jaws and more or less vertically placed teeth, and a discontinuous perignathic girdle; the interambulacral as well as the ambulacral plates continued beyond the peristome to the true mouth. Spheridia absent*" (Duncan).

Family 1. Cidaridae. Wright.

Test spheroidal; the ambulacra narrow, composed of very numerous low plates, which are usually primaries, rarely compound, each with a pair of pores arranged in single or rarely in double series; interporiferous areas with large and small granules only. Interambulacra broad, composed of few plates, most with a large primary scrobiculate tubercle, secondaries and granules. Apical system large, with five basal and five radial plates, each with a perforation. Permian to Recent; maximum in Jura and Cretaceous.

Section A. Ambulacral Pairs of Pores Uniserial.

Cidaris, Klein (Figs. 356-358). *Amb* undulating or nearly straight, the pores variable in their distance, and united by a groove or not. *IAmb* coronal plates five to eleven in each column. Apical system large. Primary spines very variable, even in the same species. Permian to Recent; chiefly Jurassic and Cretaceous.

Of this genus more than 200 species have been described. These are grouped into seven or eight artificial divisions, which are regarded by some as of sub-generic, or even generic importance. The groups may be briefly noticed as follows:—

[1] [The progress of the zoology and morphology of the recent *Echinoidea* during the last couple of decades has been such as to necessitate numerous changes in the older terminology and classification. The framing of an improved system, based upon the new grounds and expressive of the modern views entertained in regard to taxonomic relationships, was the last undertaking of the late Professor P. Martin Duncan. His essay on the "Revision of the Genera and Great Groups of the Echinoidea," published by the Linnean Society, has been of the greatest service in extending the descriptions of numerous fossil genera in the present chapter. Following the example of Lang and others, Professor Duncan's classification has been adopted almost entirely. A word of special acknowledgment is also due to Mr. W. Percy Sladen, for his advice and generous assistance in editing this portion of the *Echinodermata*.—Trans.]

(*a*) *Cidaris*, s. str. *Amb* coronal plates five to eight. *Amb* more or less undulating; pairs of pores rather close, separated by a nodule or ridge. Primary tubercles perforated and crenulated.

(*b*) *Rhabdocidaris*, Desor (Fig. 359). Test large and swollen. Poriferous zones wider than

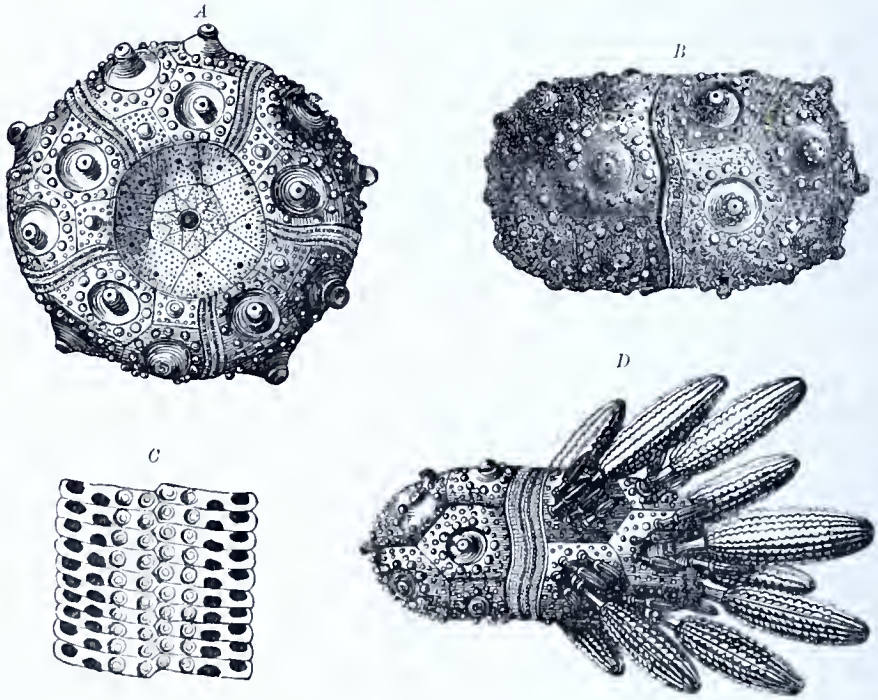

Fig. 356.

Cidaris coronata, Goldf. Upper Jura (γ); Hossingen, Wurtemberg. *A*, Dorsal aspect of test with perfectly preserved apical system. *B*, Profile. *C*, Portion of *Amb*, magnified. *D*, Partially restored view with spines attached.

in *Cidaris*, the two pores of a pair being distant and conjugated. *Amb* in general straight. Tubercles large, strongly crenulated, and more numerous than in *Cidaris*. Spines very stout,

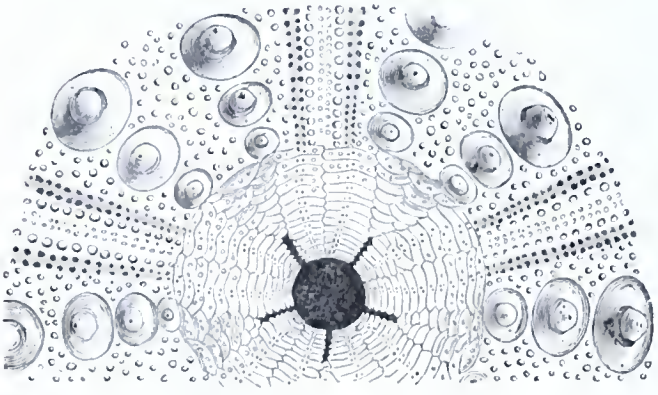

Fig. 357.

Cidaris tribuloides, Lam. Recent. Enlarged view of peristome showing plated covering.

Fig. 358.

Cidarid spines. *A*, *C. alata*, Ag. *B*, *C. dorsata*, Braun. Trias; St. Cassian, Tyrol. *C*, *C. florigemma*, Phill. Coral Rag; Wiltshire.

some cylindrical or prismatic, often spiniferous. Chiefly Jura and Cretaceous; less common in Tertiary and Recent.

(*c*) *Leiocidaris*, Desor. Like the preceding, but with uncrenulated tubercles. Spines large, smooth, cylindrical. Cretaceous to Recent.

(*d*) *Dorocidaris*, A. Ag. Like *Cidaris*, but with smooth tubercles. Recent.

(*e*) *Stephanocidaris*, A. Ag. Test thin; apical system larger than the peristome, the plates feebly united, and the whole flexible. Recent.

(*f*) *Phyllacanthus*, Brandt. Test large, swollen, and with eight to eleven *IAmb* plates. *Amb* pores in a broad zone, conjugated. Primary tubercles large, smooth, perforate. Recent.

(*g*) *Porocidaris*, Desor (Fig. 361). *Amb* broad and straight; pores wide apart, conjugated. Primary tubercles perforate and crenulate. Scrobicules transversely oval, with shallow grooves radiating from the periphery toward the centre, with or without pores at the outer extremity of the grooves. Tertiary and Recent.

(*h*) *Goniocidaris*, Desor. Test high, with numerous coronal plates, and narrow *Amb*. The median sutural regions of both areas are sunken, forming with the horizontal sutures a zigzag, with pit-like depressions at the angles. Recent.

Orthocidaris, Cott. Apical system small, pentagonal. *Amb* narrow, straight; pairs of pores in simple straight series, the pores separated by a granule. *IAmb* very broad, numerously plated. Primary tubercles small, plain, perforate, and distant. Lower Cretaceous; Europe.

Temnocidaris, Cott. Upper Cretaceous. *Polycidaris*, Quenst. Upper Jura.

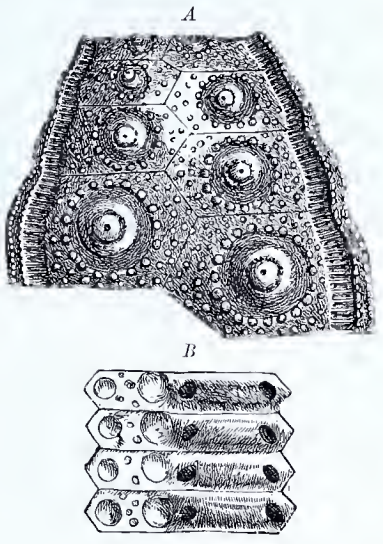

Fig. 359.

Rhabdocidaris d'Orbignyana, Desor. Upper Jura; Kelheim-Winzer, Bavaria. *A*, Fragment of test, 1/1. *B*, *Amb* plates, enlarged.

Fig. 360.

Rhabdocidaris horrida, Merian. Middle Jura. Spine, 1/1.

Fig. 361.

Porocidaris Schmiedeli, Goldf. Nummulitic Limestone; Mokkatam, near Cairo. *IAmb* plate and spine.

Section B. Ambulacral Pairs of Pores Biserial.

Diplocidaris, Desor. Test large, spheroidal. *Amb* narrow, straight; poriferous interporiferous zones of equal width. Pairs of pores very numerous, close, alternating more or less. *IAmb* broad, with seven to eight plates in each column. Primary tubercles large, perforate, scrobiculate. Upper Jura; Europe.

Tetracidaris, Cott. (Fig. 362) Remarkable in having four coronal plates in each *IAmb* at the ambitus, but diminishing to two at the apex. [It should be noticed, however, that A. Agassiz has observed a somewhat similar division in the *IAmb* plates of the recent genus *Astropyga*.] *Amb* straight, moderately broad. Poriferous zones depressed, pairs incompletely biserial; interporiferous areas narrow, granular, with a row of plain

small tubercles, placed near the borders of the poriferous zone. *IAmb* primary

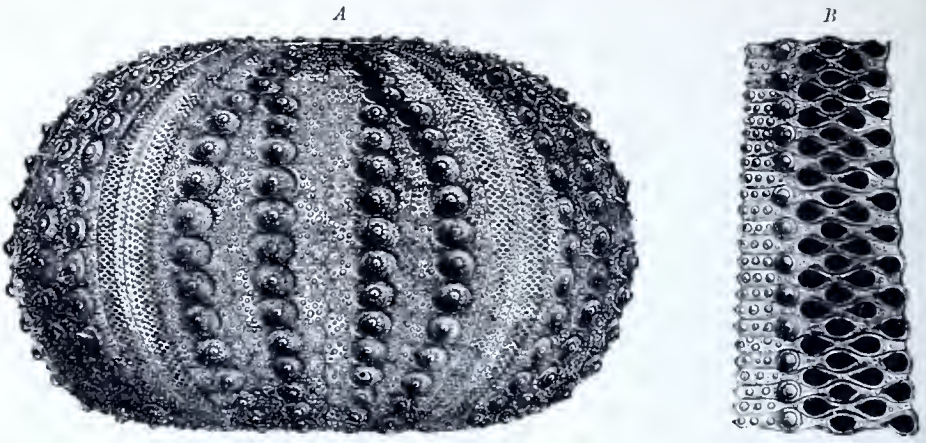

Fig. 362.

Tetracidaris Reynesi, Cotteau. Neocomian; Vergans, near Castellane, Basses Alpes. *A*, Test reduced one half. *B*, Portion of *Amb*, enlarged (after Cotteau).

tubercles very large, crenulate, and perforate. Spines narrow, elongate. Lower Cretaceous (Barrêmien); Europe.

Order 2. DIADEMATOIDA. Duncan.

"*Euechinoidea with an actinal, central peristome, and an abactinal periproct situated within the dorso-central system; with perfect or rudimentary or absent internal branchiae, with external branchiae and incisions in the peristome; with jaws and teeth and a continuous perignathic girdle; ambulacral plates alone continued beyond the peristome or as separate buccal plates. Spheridia present.*"—Duncan.

Sub-Order A. STREPTOSOMATA. Duncan.

Test more or less flexible, with external and internal branchiae. Ambulacral plates alone continued beyond the peristome to the stoma.

Family 1. Echinothuridae. Wyville Thomson.

Test thin, flexible. Coronal plates with imbricating membraneous edges. External branchiae small, internal sometimes very large. Tubercles small; spines short, cylindrical.

This family is represented by two living and two extinct genera, the latter being known only by fragmentary specimens. *Pelanechinus*, Keeping, is found in the Upper Jura, and *Echinothuria*, Woodward, in the Upper Cretaceous of England. *Phormosoma*, Wyv. Thomson, and *Asthenosoma*, Grube (*Calveria*, Wyv. Thomson), inhabit depths greater than 100 fathoms.

Sub-Order B. STEREOSOMATA. Duncan.

Test rigid, with external branchiae and rudimentary or absent internal branchiae; with isolated buccal ambulacral plates.

Family 1. **Saleniidae.** Desor (emend. Duncan and Sladen).

Apical system large, with a persistent dorso-central plate or plates, which crowd the anal orifice somewhat out of the centre of the periproct. Ambulacra narrow, with numerous, simple, low primaries; rarely compound actinally. Interambulacral plates few, with large tubercles. Teeth keeled. Spheridia present. Jura to Recent.

The presence of one or more dorso-central plates in the apical system is to be regarded as a persistent embryonic character. In all other regular Urchins, a large dorso-central plate is early developed, but becomes gradually resorbed.

Peltastes, Ag. (Fig. 344, *D*). *Amb* straight or slightly flexuous, with simple plates, and with small primary tubercles near the poriferous zones. *IAmb* broad, with large, imperforate primary tubercles, diminishing in size toward the poles. Dorso-central plate small, united to the large lateral basals, but not touching the posterior one. Upper Jura and Cretaceous.

Salenia, Gray (Fig. 363). Test small, globose, or depressed. *Amb* plates simple. Dorso-central plate in contact with all the basals; radials large, perforated at the adoral edge. Cretaceous to Recent.

Goniophorus, Agassiz. Upper Greensand. *Heterosalenia*, Cotteau. Cretaceous.

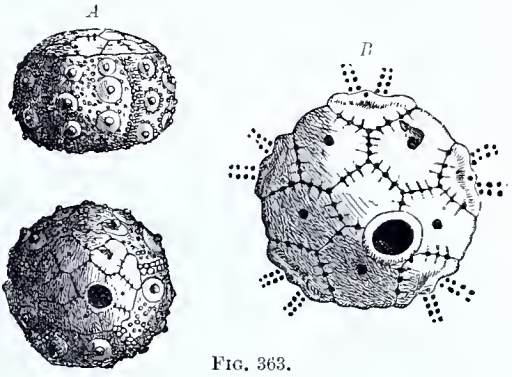

Fig. 363.

Salenia scutigera, Gray. White Chalk; Charente (after Cotteau). *A*, Lateral and dorsal aspects of test 1/1. *B*, Apical system, enlarged.

Acrosalenia, Ag. (Fig. 364). Test depressed. *Amb* plates simple primaries near the apical system, compound near the ambitus and actinally. *IAmb* tubercles large, perforate, and crenulate; those of the *Amb* much smaller, and

Fig. 364.

Acrosalenia hemicidaroides, Wright. Middle Jura; Stanton, Wiltshire. Dorsal, lateral, and ventral aspects of test, 1/1 (after Wright).

in two vertical rows. Periproct large, bounded anteriorly by the dorso-central, which is in contact with the four large anterior basals. Spines cylindrical, striated, or plain. Represented by numerous species from the Lias to the Lower Cretaceous.

Family 2. **Hemicidaridae.** Wright.

Test thick, more or less spheroidal or sub-conical. Ambulacra increasing in width actinally; the pairs of pores in arcs actinally where the plates are compound;

primary tubercles well developed. Interambulacral plates few; their primary tubercles very large at the ambitus, but decreasing in size or obsolescent toward the poles; scrobicules often coalescing. Permian to Cretaceous.

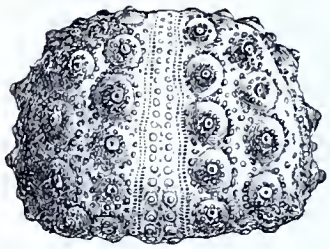

Fig. 365.

Hemicidaris crenularis, Lam. sp. Coral Rag; Châtel Censoire, Yonne. 1/1.

Hemicidaris, Ag. (Fig. 365). *Amb* narrow; plates near the apical system very numerous, small, low primaries, succeeded by plates formed of from two to four components, together with additional primary or demi-plates. Tubercles in two vertical rows, perforate and crenulate. *IAmb* broad, with two vertical rows of tubercles similar to those of the *Amb*, but much larger. Peristome large, with well-developed branchial incisions. Permian to Cretaceous.

The following sub-genera are recognised :—

(*a*) *Hemidiadema*, Ag. *Amb* tubercles large, and few in number below the ambitus, alternating distinctly. Jura and Cretaceous. *H. stramonium*, Ag.

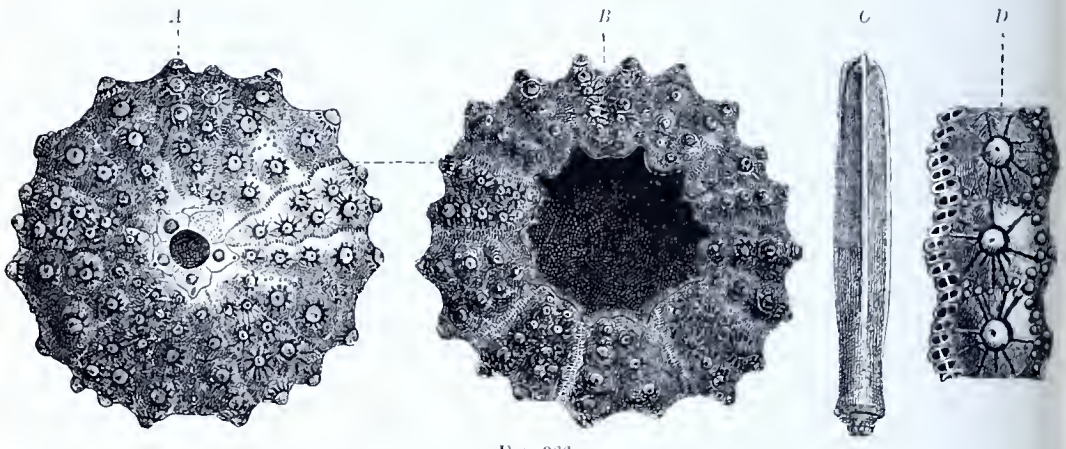

Fig. 366.

Acrocidaris nobilis, Ag. Upper Jura; St. Sulpice, near Locle, Neuchâtel. *A*, Dorsal view. *B*, Ventral view. *C*, Spine, 1/1. *D*, Three compound *Amb* plates, enlarged.

(*b*) *Hypodiadema*, Desor. *Amb* narrow, straight; their tubercles of nearly the same size throughout. Peristome and branchial incisions small. Trias to Cretaceous.

(*c*) *Pseudocidaris*, Étall. *Amb* very undulating abactinally, with primary tubercles near the peristome, granules elsewhere. Jura and Cretaceous.

Fig. 367.

Glypticus hieroglyphicus, Goldf. Coral Rag (Glyptician); Fringeli, Switzerland. 1/1.

Acrocidaris, Ag. (Fig. 366). Test large, spheroidal dorsally, flat actinally. *Amb* straight, broad at the ambitus; pairs of pores uniserial and in simple series near the apex, in arcs of from four to seven pairs near the larger tubercles, crowded and polyserial actinally. *IAmb* with two vertical rows of primary tubercles; only the largest perforate and crenulate. Spines cylindrical, often tricarinate. Upper Jura and Cretaceous.

Goniopygus, Ag. Apical disk large, plates more or less ornamented; basal plates punctured on adoral margin. Peristome very large, with small branchial incisions. Cretaceous and Eocene.

Glypticus, Ag. (Fig. 367). *Amb* straight, and narrow except at the peristome, where the poriferous zones are expanded; with two vertical rows of

small, smooth, primary tubercles. *IAmb* tubercles replaced abactinally by warty or irregular elongate elevations. Epistroma much developed. Abundant in Upper Jura.

Family 3. **Diadematidae.** Wright.

Test highly ornamented, tumid, depressed, or spheroidal. Ambulacra straight, moderately broad or narrow, with vertical rows of small primary tubercles, and compound plates near the ambitus and actinally. Interambulacra broad, with numerous low plates; the rows of primary tubercles diminishing in number dorsally. Peristome large, polygonal. Lias to Recent.

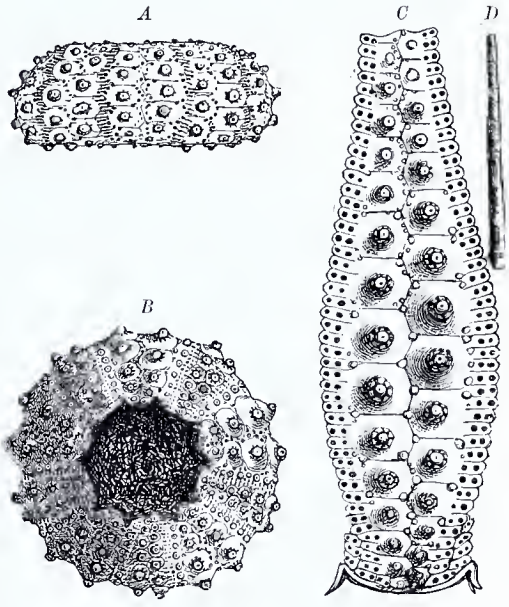

Fig. 368.

Diadema (*Pseudodiadema*) *neglectum*, Thurm. From the Bernese Jura. *A*, *B*, Profile and ventral aspect of test, 1/1. *C*, Ambulacrum, enlarged. *D*, Spine, 1/1.

Sub-Family A. Diadematinae.

Ambulacral plates compound near the ambitus; pairs of pores in simple vertical series or in arcs of three.

Diadema, Schynvoet (*Pseudodiadema*, Desor), (Fig. 368). *Amb* narrow, often projecting; two vertical rows of small, primary, crenulate, and perforate tubercles extending from peristome to apex. *IAmb* with two or more vertical rows of primary tubercles resembling those of the *Amb*, but larger. Secondary tubercles and granules surrounding the scrobicules. Spines long, hollow, longitudinally striated. Lias to Recent.

Duncan has shown that the separation of the fossil species from the recent under Desor's term of *Pseudodiadema* is a purely artificial distinction. The following sub-genera are recognised:—*Centrostephanus*, Peters; Recent. *Micrediadema*, Cotteau; Lias. *Diademopsis*,

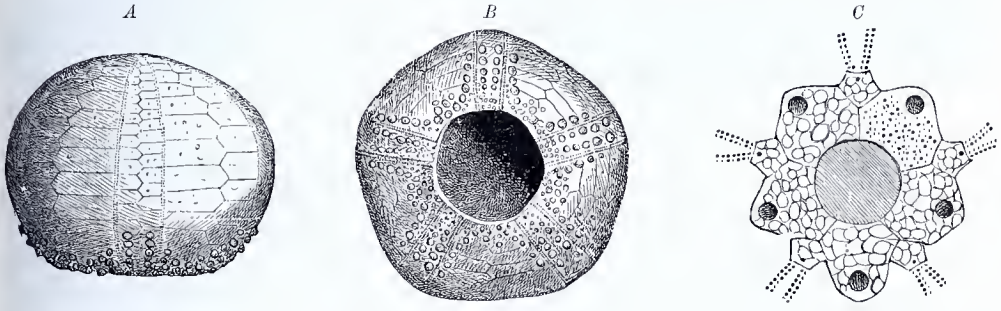

Fig. 369.

Codiopsis doma, Desm. sp. Cenomanian (Tourtia); Tournay, Belgium. *A*, Side-view of test, 1/1. *B*, Ventral aspect of same. *C*, Apical system, enlarged.

Desor; Lias. *Echinodiadema*, Cotteau; Upper Jura. *Hemipedina*, Wright; Jura, Cretaceous, and Recent. The latter differs from *Diadema* in having simple *Amb* plates near the apex, and perforate, but not crenulate tubercles.

Heterodiadema, Cott. Like *Diadema*, but with the apical system greatly

extended into the depressed posterior *IAmb*. Pairs of basal plates separated by the antero-lateral radials, the fifth basal absent. Cretaceous. *H. libycum*, Cotteau.

Codiopsis, Ag. (Fig. 369). Primary tubercles of both areas small, smooth, nearly equal in size, and only occurring actinally and for a short distance toward the ambitus. Pairs of pores uniserial. Cretaceous.

Cottaldia, Desor. Cretaceous and (?) Recent. *Pleurodiadema*, de Loriol. Jura. *Magnosia*, Michelin. Jura and Cretaceous.

Sub-Family B. Diplopodiinae.

Ambulacral plates compound; pairs of pores biserial.

Diplopodia, M'Coy. *Amb* narrow, with two vertical rows of perforate and crenulate primary tubercles. Pairs of pores in double vertical series near the poles, uniserial at the ambitus. Jura and Cretaceous.

Pedinopsis, Cotteau. Cretaceous. *Phymechinus*, Desor. Jura.

Sub-Family C. Pedininae.

Ambulacral plates compound; pairs of pores triserial.

Pedina, Ag. *Amb* narrow, poriferous zones wide. Both areas with two vertical rows of small, perforate, primary tubercles. Upper Jura.

Pseudopedina, Cott. Like the preceding, but with larger primary

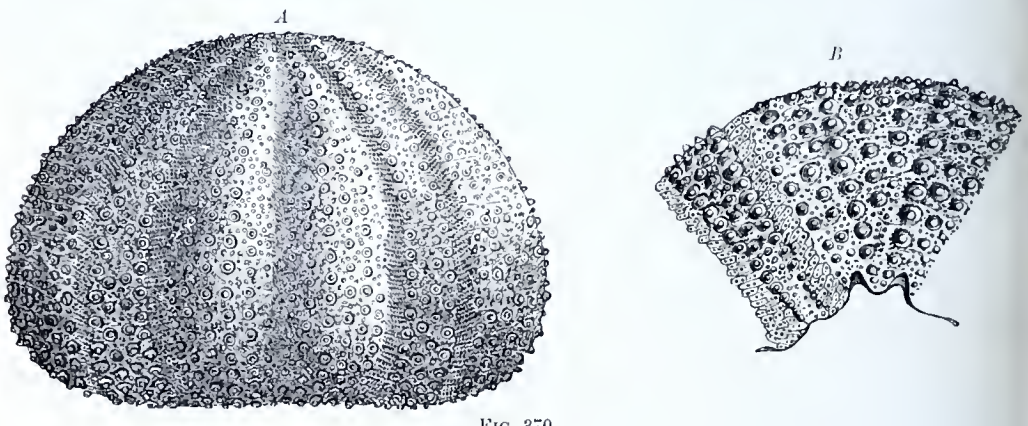

Fig. 370.

Stomechinus lineatus, Goldf. sp. Coral Rag; Sontheim, Wurtemberg. *A*, Side-view of test, 1/1. *B*, Portion of actinal surface.

tubercles, which are present in the *Amb* near the ambitus only. Upper Jura.

Micropedina, Cott. *Amb* with several, and *IAmb* with numerous vertical rows of very small primary tubercles. Cretaceous.

Stomechinus, Desor (Fig. 370). Distinguished from *Pedina* by its wider *Amb*, and imperforate, non-crenulate, primary tubercules. Secondary tubercles and granules often present. Jura and Cretaceous.

Codechinus, Desor. Tubercles very small, plain, irregularly distributed. Cretaceous.

Polycyphus, Ag. Jura. *Astropyga*, Gray. Recent.

Sub-Family D. Orthopsinae.

Ambulacra with simple primary plates; pairs of pores in simple series.

Orthopsis, Cott. *Amb* much narrower than the *IAmb*, straight, and with numerous pairs of pores in straight series. *Amb* with two, *IAmb* with several vertical rows of small, plain, perforate tubercles. Jura and Cretaceous.

Eodiadema, Duncan. Lias; England. *Echinopsis*, Ag. Eocene; Europe and Egypt.

Family 4. **Cyphosomatidae.**

Test highly ornamented, moderate in size. Ambulacra with high compound plates, each with three to seven pairs of pores in an arc; the pairs sometimes biserial near the apical system, and crowded near the peristome. The adoral and supra-adoral components of the plates are primaries, and the others demi-plates. Ambulacra with two vertical rows of primary tubercles; interambulacra with a variable number. Jura to Recent.

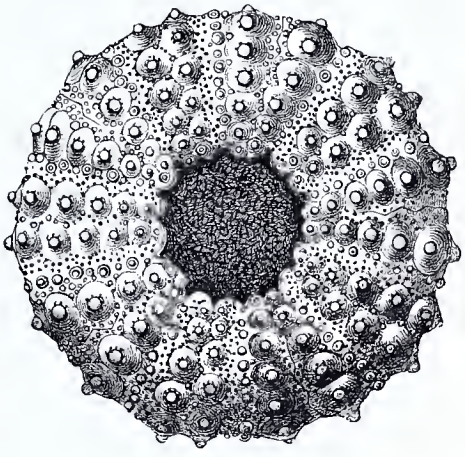

Fig. 371.

Cyphosoma Koenigi, Mantell. White Chalk; Sussex. Ventral aspect, 1/1.

Cyphosoma, Ag. (Fig. 371). Test depressed, with few coronal plates. *Amb* with well-developed poriferous zones, undulating. Pairs of pores biserial at the apex, crowded at the peristome. *IAmb* broader than the *Amb*, with two or more vertical rows of primary tubercles, which are imperforate and crenulate, like those of the *Amb*. Apical system encroaching upon the posterior *IAmb*. Jura to Recent.

Micropsis, Cott. *Amb* with three to five pairs of pores to a compound plate, and two or more vertical rows of small primary tubercles, which are perforate and crenulate. Cretaceous and Eocene.

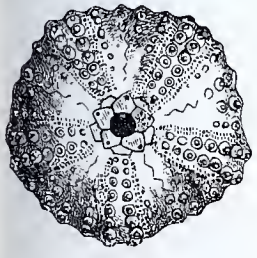

Fig. 372.

Coelopleurus equis, Ag. Eocene; Biarritz, France. 1/1.

Family 5. **Arbaciidae.** Gray

Test depressed dorsally, flat actinally. Ambulacra narrow, straight, expanding near the peristome, with compound plates near the ambitus. Pairs of pores simple or in large arcs, sometimes crowded actinally. Interambulacra with few or several vertical rows of imperforate, non-crenulate, primary tubercles with expanded bosses. Tertiary and Recent.

Arbacia, Gray. Tertiary and Recent. *Echinocidaris*, Duncan and Sladen (*non* Desmoulins). Recent.

Coelopleurus, Ag. (Fig. 372). *Amb* with two vertical rows of plain, primary tubercles placed on flat scrobicules, diminishing in size toward the apex, and sometimes replaced there by granules. *IAmb* with a large bare median area abactinally; the tubercles largest at the

ambitus, sometimes disappearing toward the apical system. Tertiary and Recent.

Podocidaris, A. Ag. Recent; Caribbean Sea and Philippines.

Family 6. **Temnopleuridae.**

Test highly ornamented, tumid, or spheroidal. Ambulacra with triple compound plates, united with the interambulacral plates by grooved and sometimes pitted sutures. All plates of the test, except the component ambulacral plates, united by a dowelling of knobs and sockets. Cretaceous to Recent.

Glyphocyphus, Haime. Test small, depressed spheroidal. *Amb* narrow, straight, with two vertical rows of small, perforate, crenulate, primary tubercles, and numerous miliaries. *IAmb* broad, with two rows of primaries somewhat larger than those of the *Amb*. Transverse and median sutures grooved. Cretaceous and Eocene.

Dictyopleurus, Duncan and Sladen. Eocene; Asia and Europe. Egypt. *Paradoxechinus*, Laube. Miocene; Australia. *Echinocyphus*, Cott., and *Zeuglopleurus*, Gregory. Cretaceous; Europe.

Temnopleurus, Ag. Transverse sutures of all plates grooved and pitted. Apical system small, compact, slightly projecting. Tertiary and Recent.

Temnechinus, Forbes. Test small, subglobose, depressed abactinally. Both areas with two vertical rows of plain primaries. Apical system prominent, compact, the sutures between the plates more or less grooved. Late Tertiary and Recent.

Salmacis, Ag. Eocene, Pliocene, and Recent. *Microcyphus*, *Amblypneustes*, and *Holopneustes*, Ag. Recent.

Family 7. **Echinometridae.** Gray (emend. A. Agassiz).

Test large, either symmetrical and polyporous, or with the long axis not coinciding with the antero-posterior axis, and the compound ambulacral plates with three or more pairs of pores. Teeth keeled. Tertiary and Recent.

Heterocentrotus, *Colobocentrotus*, Brandt; and *Echinometra*, Rondelet. Recent.

Stomopneustes, Ag. (*Heliocidaris*, Desm.), (Fig. 373). Antero-posterior axis forming an angle with the major diameter. *Amb* straight, with pores in arcs of three pairs dorsally, crowded and triserial below the ambitus. Both areas with two vertical rows of plain tubercles, diminishing actinally and dorsally. Tertiary and Recent.

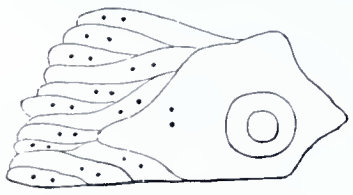

Fig. 373.

Stomopneustes variolaris, Ag. Compound *Amb* plate.

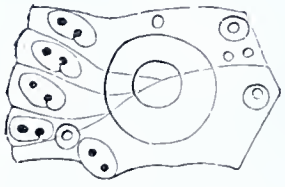

Fig. 374.

Strongylocentrotus Drocbachiensis, Müll. sp. Compound *Amb* plate.

Strongylocentrotus, Brandt (Fig. 374). Test symmetrical and polyporous. *Amb* straight, broad at the ambitus and peristome, and with broad poriferous zones. Pairs of pores in oblique arcs, or almost transverse series of from four to ten pairs, and crowded actinally. Interporiferous areas with two vertical rows of plain, imperforate primary tubercles; secondaries and miliaries also

present. *IAmb* with two rows of primary, and four or more of secondary tubercles. Late Tertiary and Recent.

Sphaereehinus, Desor. *Amb* straight, wide. Pairs of pores in arcs or oblique lines of four to eight pairs, polyserial actinally. Interporiferous areas with two to six vertical rows of plain, imperforate primaries, and horizontal rows of secondary tubercles and miliaries. *IAmb* with two to twelve vertical rows of primaries. Pliocene and Recent.

Eurypneustes, *Aeolopneustes*, Duncan and Sladen. Eocene ; Asia.

Family 8. **Echinidae.** Wright.

Test symmetrieal ; ambulacra and interambulaera of equal width. Ambulaeral plates eompound, with three pairs of pores, whieh are arranged in high or low ares of triplets. Coronal plates without pits and grooves, and their opposed surfaees plain. Teeth keeled. Cretaceous to Recent.

Eehinus, Rond. *Amb* straight, with narrow poriferous zones ; pore pairs in more or less vertical arcs of triplets. Interporiferous areas with two vertical rows of small, plain, primary tubercles, with or without irregularly placed secondary tubercles and primaries. *IAmb* with two vertical rows of primaries, and few or numerous rows of secondary tubercles and miliaries. Peristome small, circular ; the buccal membrane with ten buccal plates bearing tentacles and small spines. Cretaceous to Recent.

Subgenus *Psammechinus*, Ag. Like *Echinus*, but the buccal membrane with numerous concentric plates, besides the ten buccal plates. Cretaceous to Recent.

Stireehinus, Desor. Both areas with two rows of large, plain, primary tubercles situated on raised keel-like projections. Pliocene ; Europe.

Glypteehinus, de Loriol. Cretaceous. *Tripneustes*, Ag. Miocene and Recent.

Leiopedina, Cott. (*Chrysomelon*, Laube). Test large, melon-shaped. *Amb* long, straight, very broad. Poriferous zones broad, pairs of pores triserial, and almost horizontal. Plates very numerous, low, broad, compound. Tubercles small, plain, finely perforate, in two distant vertical rows. *IAmb* broad, with two rows of tubercles similar to the ambulacral, and with intermediate granules. Eocene.

Hypeehinus, Desor. Tertiary. *Toxopneustes*, A. Ag. (*non* Ag.) Recent. *Boletia*, Desor. Recent.

Order 3. HOLECTYPOIDA. Duncan.

"*Euechinoidea with an aetinal, eentral peristome, and the periproet situated beyond the dorso-eentral system in the posterior interambulaerum ; with external branchiae ; with a pair of pores or only one pore to an ambulaeral plate ; with feeble jaws and vertieal teeth, or without these struetnres ; with a variably eonstrueted perignathie girdle. Spheridia present.*"—Duncan.

Section I.—*Perignathie proeesses of the ambulaera present.*

Holectypus, Desor (Fig. 375). *Amb* narrow, straight, widest at the ambitus ; some of the plates compound. *IAmb* with rather large plates, and many rows of tubercles. Peristome large, decagonal, with well-marked branchial incisions, jaws, and feeble perignathic girdle. Periproct large,

pyriform, situated between the peristome and posterior edge of the test. Apical system small, central. Jura and Cretaceous.

Pileus, Desor. Test large, sub-hemispherical dorsally, flat actinally.

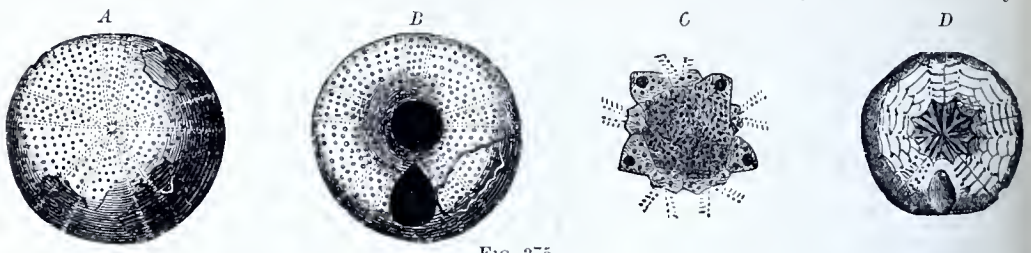

Fig. 375.

A, *B*, *Holectypus orificatus*, Schlot. Upper Jura; Streitberg, Franconia. *C*, *D*, *H. depressus*, Leske sp. Middle Jura; France. Apical system and ventral surface (after Cotteau).

Tubercles small, irregularly arranged. Periproct supra-marginal, small, broadly ovoid. Upper Jura.

Pygaster, Ag. (Fig. 376). Test large, depressed dorsally, concave actinally. *Amb* straight, similar, flush or slightly raised, widest at the ambitus. Poriferous zones straight, simple, narrow; tubercles of interporiferous areas in two or four vertical rows; those of the *IAmb* in horizontal rows. Peristome large, decagonal, with jaws and feeble perignathic girdle. Periproct immediately beyond the apical system. Jura and Cretaceous.

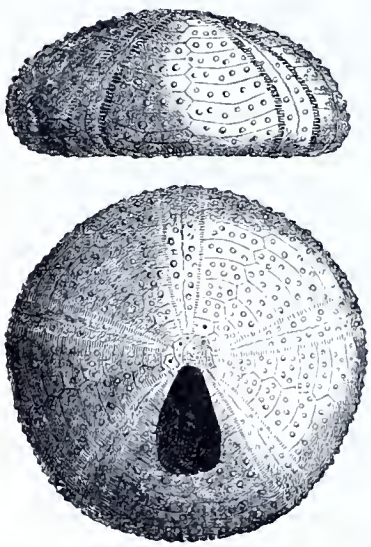

Fig. 376.

Pygaster umbrella, Ag. Oxfordian; Châtillon-sur-Seine. Young individual, $^1/_1$ (after Cotteau).

Section II.—*Perignathic girdle with well-developed interambulacral ridges; ambulacral processes rudimentary or absent.*

Discoidea, Klein (Fig. 377). Test hemispherical above the margin, flat actinally. *Amb* narrow, with some compound plates near the ambitus and actinally; pairs of pores very numerous, small. *IAmb* with distinct median sutures, and small, perforate, and crenulate tubercles. Plates within the actinal surface with radiating ribs, ten in all, extending as far as the peristome; appearing on casts as deep depressions. Periproct small, infra-marginal. Cretaceous.

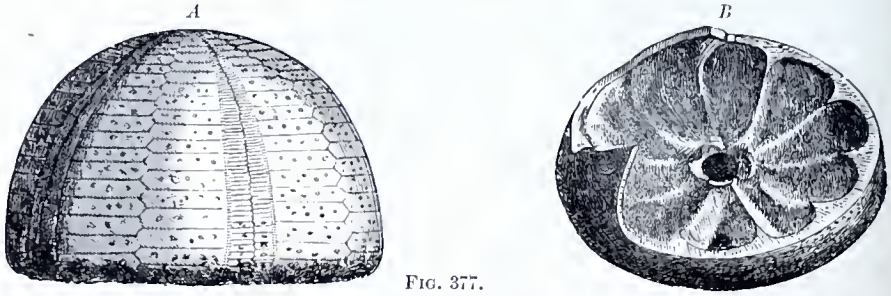

Fig. 377.

Discoidea cylindrica, Ag. Upper Cretaceous; Lüneburg. *A*, Side-view. *B*, Test broken open to show the inner partitions, $^1/_1$.

Conoclypeus, Ag. (Fig. 378). Test large, thick; conical or vaulted dorsally,

rather flat actinally. *Amb* long, open, with broad poriferous zones nearly to ambitus, narrowing thence to peristome. Pores wide apart and in pairs where

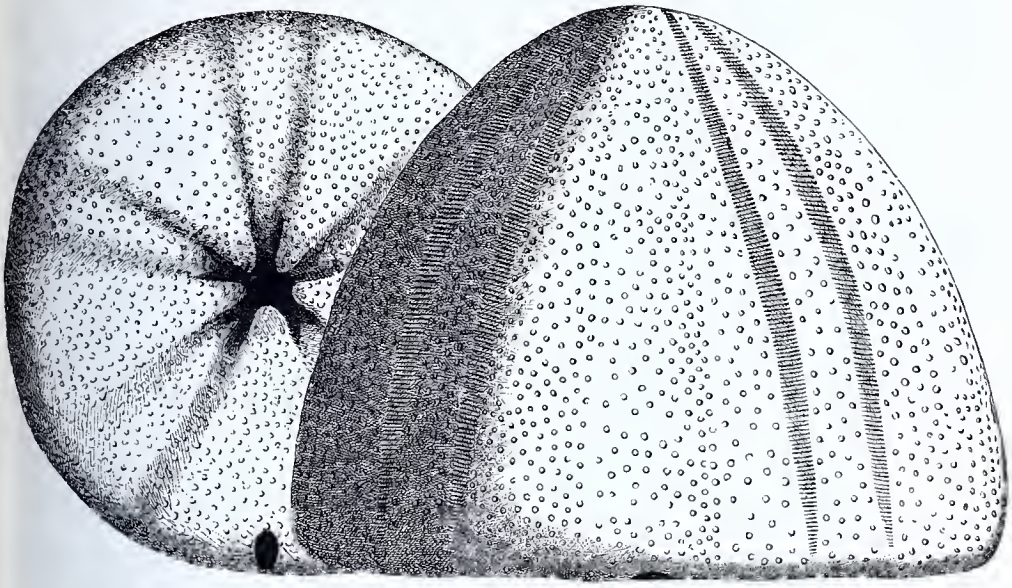

Fig. 378.

Conoclypeus conoideus, Goldf. sp. Eocene; Kressenberg, Bavaria (2/3 natural size).

the zones are broad; the pairs separated by costae. Pores continued in single series over the ambitus as far as the central, pentagonal peristome. Periproct infra-marginal, oval (?). Cretaceous; Eocene.

Galeropygus, Cotteau; *Pachyclypeus*, Desor. Upper Jura; Europe.

Order 4. CLYPEASTROIDA. Duncan.

"*Euechinoidea with an actinal peristome, a periproct situated beyond the dorso-central system, in the posterior interambulacrum; with external branchiae; with tentacular pores in the interambulacra, and more than a pair to an ambulacral plate; tentacles heteropodous in arrangement; with more or less horizontal and rarely vertical teeth, and with jaws situated superiorly to the disconnected perignathic girdle. Spheridia few, covered.*"—Duncan.

Family 1. **Fibulariidae.** Gray (emend. Duncan).

Test small, with rudimentary, widely open, few-pored petals. Interambulacra small, with a single apical and a single peristomial plate. Ambulacra limited actinally on the interior of the test by low vertical partitions at their sides, radiating toward the peristome. Perignathic processes broad, low, one on each interambulacrum. Periproct usually actinal. Cretaceous to Recent.

Echinocyamus, van Phels. Test thick, depressed, pyriform or sub-circular in outline, concave actinally. *Amb* broader than the *IAmb*, short where slightly petaloid, widely open distally; pairs of pores few and increasingly

far apart. Peristome central, pentagonal, with small jaws. Periproct between the peristome and posterior edge of the test. Cretaceous to Recent.

Fig. 379.

Echinocyamus placentus, Goldf. sp. (*E. siculus*, Ag.) Pliocene; Sicily. 1/1.

Sub-genus.—*Scutellina*, Ag. Periproct small, marginal, or more or less supra- or infra-marginal. Tertiary.

Sismondia, Desor. Test sub-pentagonal or ovoid, depressed, inflated at the margin. Petaloid parts of the *Amb* usually long, more or less open; pairs of pores not continued actinally. Tubercles minute. Eocene and Miocene.

Fig. 380.

Fibularia subglobosa, Goldf. sp. Upper Cretaceous; Maestricht. 1/1.

Fibularia, Lam. (Fig. 380). Test thin, ovoid, tumid dorsally and at the side. *Amb* short; pairs of pores very few, continued wide apart to the margin, non-conjugated. Peristome and periproct small, sunken, close together. Upper Cretaceous and Recent.

Runa, Ag. Tertiary; Europe.

Family 2. **Clypeastridae.** Agassiz.

Test small to very large, depressed, flat, or high. Petaloid parts of the ambulacra highly developed, usually unequal; the actinal furrows straight. Interambulacra actinally discontinuous; one peristomial and two apical plates in each. Perignathic processes tall, narrow, two on each ambulacrum, fitting in below the large jaws. Peristome central, pentagonal; periproct small, marginal or infra-marginal. Internal structure with needles, pillars, and other processes extending from floor to roof, especially near the edge of the test; sometimes these are fused to form concentric partitions, and the ambulacra may also be protected by an inner wall. Tertiary and Recent.

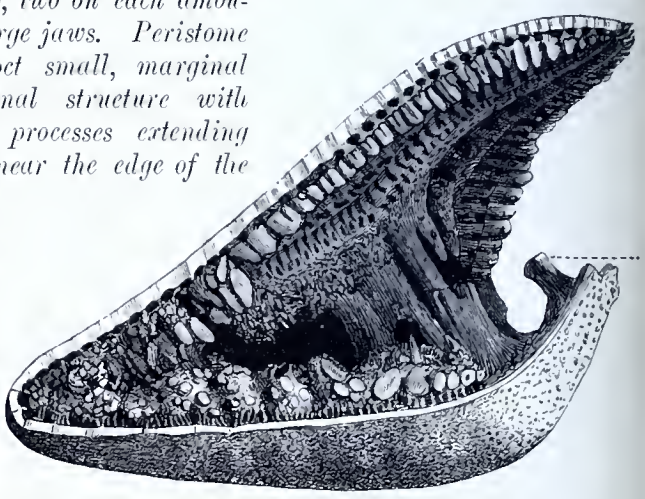

Fig. 381.

Clypeaster Aegyptiacus, Mich. Pliocene; Gizeh, near Cairo. Fragment showing internal calcareous deposits. *au*, Auricles.

Clypeaster, Lam. (Figs. 381, 382). Actinal surface flat, with the peristome suddenly deeply sunken; edge thin, undulating in contour, with or without re-entering angles. Petals long, broad, tumid; pores wide apart, unequal, conjugated. Periproct near or at the edge. Internal structure not forming a double wall covering the *Amb*. Tertiary and Recent.

This genus includes some of the largest Sea-urchins known. Recent species are littoral, or shallow water inhabitants.

Diplothecanthus, Duncan (*Echinanthus*, Breyn. p.p.) Margin and actinal surface tumid, but hollow from the margin to a deep central peristome. In-

ternal structure investing the *Amb* with a double wall, but not forming concentric partitions near the edge. Tertiary and Recent.

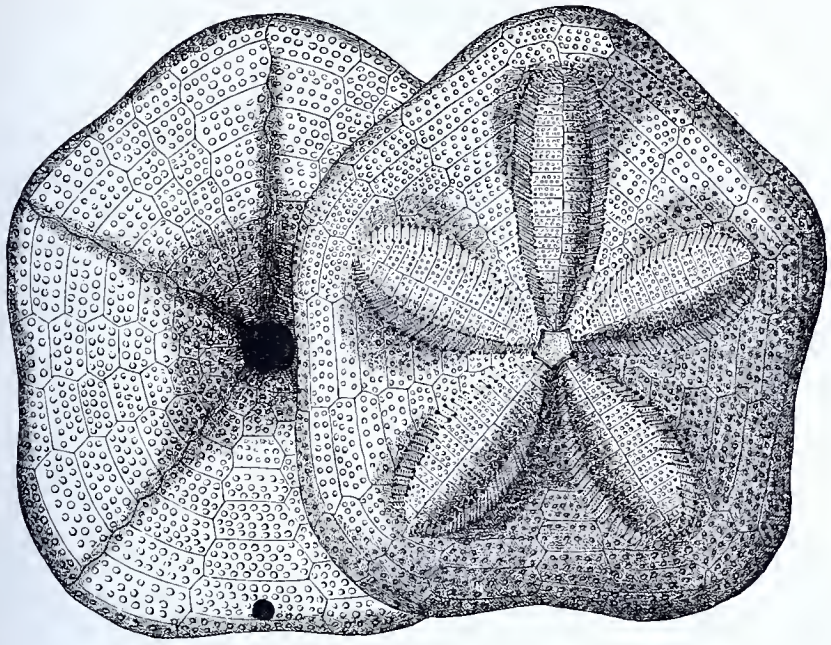

Fig. 382.

Clypeaster grandiflorus, Bronn. Miocene; Boutonnet, near Montpellier. 1/2 natural size (after Desor).

Plesianthus, Duncan; *Anomalanthus*, Bell. Recent.

Laganum, Klein. Belongs properly to a separate family or sub-family. Tertiary and Recent.

Family 3. **Scutellidae.** Agassiz.

Test very flat, with entire or incised margin; lunules or slits in the areas or not. Ambulacral furrows bifurcating and branching. Peristome flush; jaws flat, teeth superior. Radiating partitions between the floors internally. Tertiary and Recent.

Scutella, Lam. (Fig. 383). Test circular or sub-circular in outline, sometimes undulating or notched, broadest behind. Petaloid parts of the *Amb* unequal, well-developed, nearly closed. Peristome small, central, sub-circular. Periproct very small, infra-marginal. Apical system central, more or less pentagonal. Tertiary.

Sub-genus.—*Echinaraehnius*, Leske (*Dendraster*, Ag.) Apical system eccentric in front or behind. Periproct actinal, marginal or supra-marginal. Recent.

Echinodiscus, Breyn. (*Amphiope*, *Lobophora*, Ag.) Like *Scutella*, but truncated posteriorly, and with two round or elongate lunules or slits there, one in each of the median lines of the postero-lateral *Amb*. Tertiary and Recent.

Encope, Ag. Test with a broad notch or a lunule in the median line of each *Amb*, and a lunule in the posterior *IAmb*. Miocene and Recent.

Mellita, Klein. Test very flat, with five or six usually closed lunules,

more rarely cuts; one in the median line of the posterior *IAmb*, the others

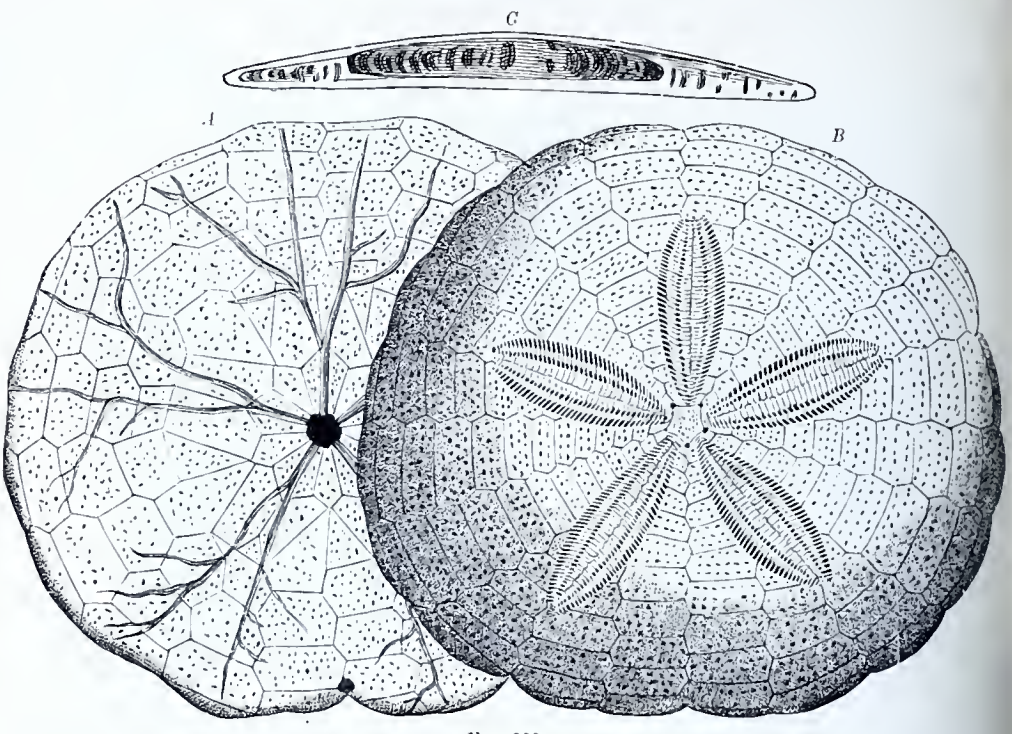

Fig. 383.

Scutella subrotundata, Lam. Miocene; Bordeaux. *A*, *B*, Ventral and dorsal aspects. *C*, Section, 1/1.

in the *Amb*. *Amb* petaloid dorsally, the posterior pair the longest. Pliocene and Recent.

Lenita, Desor. Eocene. *Rotula*, Klein. Recent. *Arachnoides*, Breyn. (*Asterodaspis*, Conrad). Pliocene and Recent.

Order 5. SPATANGOIDA. Duncan.

"*Eucchinoidea with an actinal or a frontal peristome, and a periproct situated beyond the dorso-central system, in the posterior interambulacrum; without external branchiae; jaws, teeth, and perignathic girdle. Spheridia numerous.*"—Duncan.

Sub-Order A. CASSIDULOIDEA. Duncan.

Ambulacra abactinally simple, petaloid or sub-petaloid, usually similar. Some or all of the interambulacra with a single peristomial plate; the postero-lateral areas symmetrical actinally, without any fusion of plates; no plastrons. Peristome variously shaped, with or without floscelles.

Family 1. Echinoneidae. Wright.

Test tall, or low and tumid dorsally; tumid and rarely flat actinally. Apical system central, compact, with four perforated basals. Ambulacra similar, dorsally apetalous or sub-petaloid. Pores in simple pairs or in oblique triplets actinally; no floscelle. Peristome oblique or transversely elliptical, rarely symmetrical. Periproct actinal, marginal or supra-marginal. Cretaceous to Recent.

Sub-Family A. Echinoconinae. Duncan.

Tall, conical, or sub-hemispherical tests, rather flat actinally. Ambulacra with pairs of pores in oblique triplets actinally.

Echinoconus, Breyn. (*Galerites*, Lam.) *Amb* flush or slightly raised, apetalous, straight; some of the plates compound. Peristome sunken, slightly decagonal, symmetrical. Perignathic girdle indicated by a thickening of the *IAmb* as a low false ridge. Abundant in the Lower and Middle Cretaceous.

Lanieria, Duncan. Cretaceous or Eocene; Cuba.

Sub-Family B. Echinoneïnae. Desor.

Test low, tumid, and more or less pulvinate actinally; peristome central or subcentral and oblique.

Echinoneus, van Phels. *Amb* narrow, actinally unequally broad, owing to obliquity of the large, triangular peristome. Miocene to Recent.

Caratomus, Ag. Cretaceous. *Amblypygus*, Ag. Tertiary.

Pygaulus, Ag. (Fig. 384). Test small, thick; apical system slightly

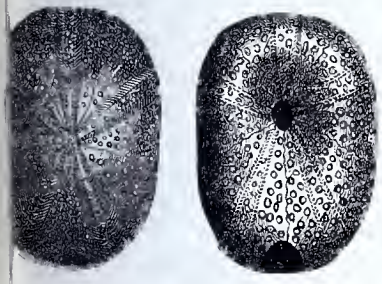

Fig. 384.

Pygaulus Desmoulinsi, Ag. Urgonian (Schrattenkalk); Säntis, Switzerland. 1/1.

Fig 385.

Pyrina incisa, Ag. sp. Neocomian (Hils); Berklingen, Brunswick. 1/1.

eccentric in front. *Amb* narrow, widest at the ambitus; pairs of pores in simple series, conjugated; the pores of a pair sometimes differently shaped. Cretaceous.

Pyrina, Desm. (Fig. 385). Like the preceding, but pores non-conjugated, and the pairs separated by costae. Cretaceous and Eocene.

Anorthopygus, Cotteau. Cretaceous (Cenomanian); Europe.

Sub-Family C. Echinobrissinae. Duncan.

Test depressed, elongate, tumid. Ambulacra sub-petaloid. Apical system and peristome eccentric; floscelle absent or rudimentary. Interambulacra entering the peristomial margin with a single plate. Periproct supra-marginal.

Echinobrissus, Breyn. (*Nucleolites*, Lam.), (Fig. 386). Test ovate, rounded in front, broadest and more or less truncated behind; or rectangular, with the angles rounded; or sub-circular; concave actinally. *Amb* unequal, open at the end of the sub-petaloid parts; pairs of pores in simple series, more or less unequal in shape and size, the outer ones elongate; below the sub-petaloid parts the pores are in small oblique pairs, conjugate or not. Periproct at

upper end of a groove situated on the abactinal area of the test. Abundant in Upper Jura and Cretaceous; present also in Eocene and late Tertiary.

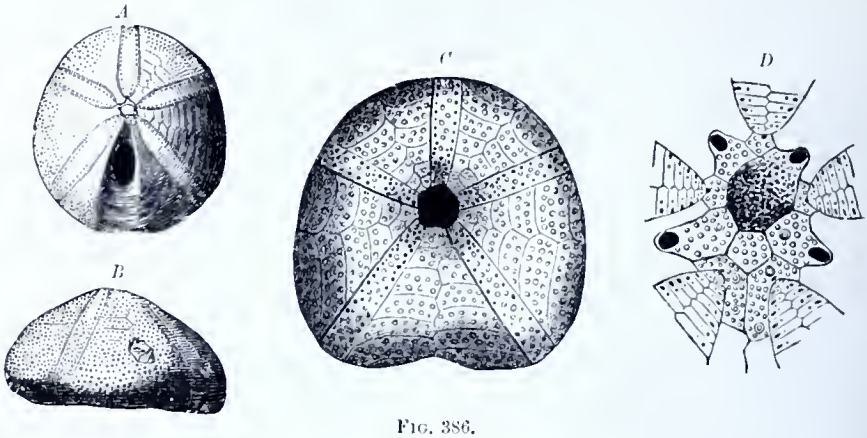

Fig. 386.

A, B, Echinobrissus clunicularis, Llhwyd sp. Cornbrash; Egg, Aargau. 1/1. *C, D, E. scutatus*, Lam. sp. Upper Oxfordian; Trouville, Calvados. *C*, Ventral aspect of large individual. *D*, Apical system, enlarged (after Cotteau).

Sub-genus *Dochmostoma*, Duncan (*Trematopygus*, d'Orb.) Like the preceding, but with oblique peristome. Cretaceous.

Botriopygus, d'Orb. Cretaceous. *Ilariona*, Dames. Eocene.

Family 2. **Cassidulidae.** Agassiz.

Test variable in shape. Ambulacra petaloid, sub-petaloid, or apetalous dorsally, and with crowded doubling of the pairs of pores close to the peristomial margin, forming with the single, swollen, and ornamented interambulacral peristomial plates a floscelle. Jura to Recent.

Cassidulus, Lam. (Fig. 387). Test small, oblong, depressed, convex dorsally, flat actinally. *Amb* short, sub-petaloid, not closing; pores continued from the middle part to the well-developed floscelle. Peristome eccentric in front; periproct supra-marginal, longitudinally elongated. Cretaceous and Eocene.

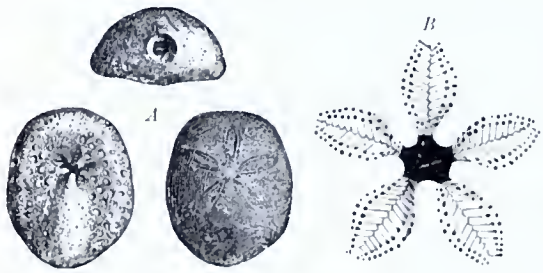

Fig. 387.

Cassidulus lapis-cancri, Lam. *A*, Test in three positions. *B*, Floscelle, enlarged.

Sub-genus *Rhynchopygus*, d'Orb. Periproct transversely elongate, with overhanging rostrum. Cretaceous to Recent.

Sub-genus *Pygorhynchus*, Ag. Test concave actinally, with long petals. Peristome and periproct longest transversely. Cretaceous to Miocene.

Echinanthus, Breyn. Test thin, ovoid, low, convex dorsally, and concave actinally. *Amb* unequal, petaloid, usually short. Peristome eccentric in front, with well-developed pentagonal floscelle. Periproct oval, marginal or supra-marginal, at the top of a longitudinal groove. Upper Cretaceous and Eocene.

Stigmatopygus, d'Orb. Cretaceous. *Eurhodia*, d'Arch. and Haime. Eocene. *Paralampas* and *Neocatopygus*, Duncan and Sladen. Eocene. *Catopygus*, Ag.

Cretaceous. *Studeria*, Duncan. Tertiary and Recent. *Phyllobrissus*, Cotteau. Jura and Cretaceous.

Clypeus, Klein. Test large, low, nearly flat actinally. *Amb* wide, petaloid, not closing dorsally, narrow at the ambitus and actinally. Pairs of pores in

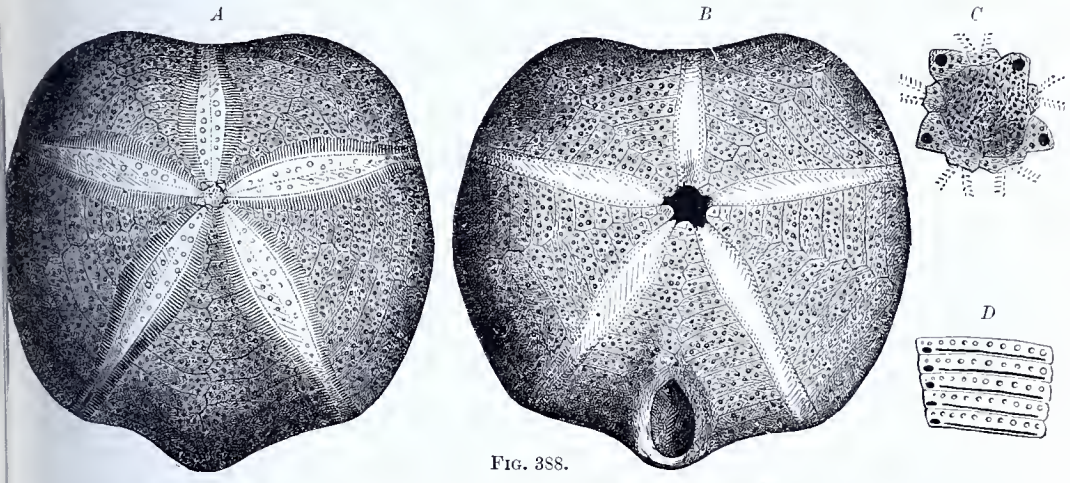

Fig. 388.

Pygurus Royerianus, Cott. Kimmeridgian; Tönnjesberg, near Hanover. *A*, *B*, Dorsal and ventral views of test, $^3/_4$ natural size. *C*, Apical system, enlarged. *D*, Ambulacral plate, magnified.

the petaloid parts with the inner pore small and circular, the outer transversely elongate, and in a long groove. Periproct high up, usually in a groove along the median line of the posterior *Amb*. Upper Jura.

Pygurus, Ag. (Fig. 388). Test large, angular, rounded, or cordiform in marginal contour; depressed or rather tall and sub-conical dorsally. *Amb*

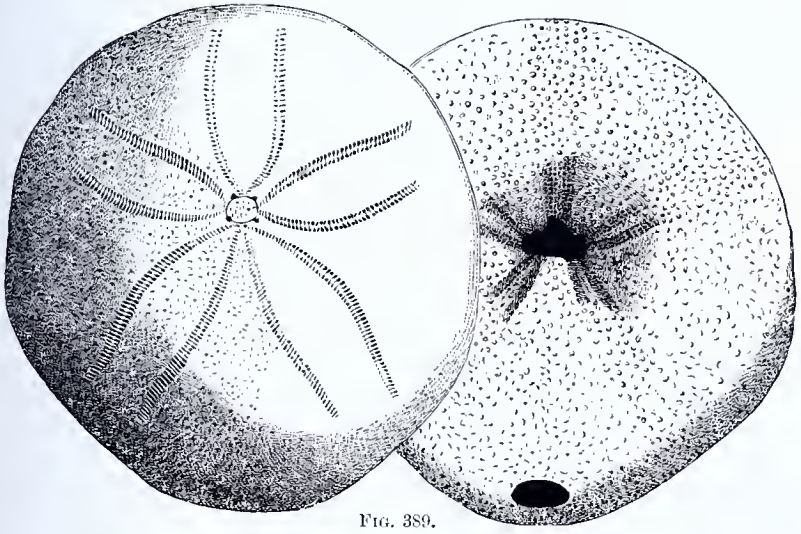

Fig. 389.

Echinolampas Kleini, Goldf. Oligocene; Doberg, near Bunde. $^1/_1$.

flush dorsally, unequal, long; the petaloid parts contracting but not closing marginally, and expanding again actinally, where the *Amb* are grooved. Periproct infra-marginal, pyriform or ovoid, in a special area or rostrum close to the posterior edge of the test. Upper Jura and Cretaceous.

Echinolampas, Gray (Fig. 389). Test variable in size and shape, more or less ovoid or circular at the tumid marginal outline; tall and conical or

depressed dorsally. *Amb* petaloid for a variable distance; pores of the petals differing in shape, conjugated, and continued beyond in simple series. Peristome slightly in front, or sometimes central. Periproct transversely elliptical, infra-marginal. Widespread in Tertiary and Recent.

Conolampas, *Neolampas*, A. Ag. Recent. *Plesiolampas*, Duncan and Sladen. Eocene. *Palaeolampas*, Bell. Upper Cretaceous and Tertiary.

Family 3. **Collyritidae.** d'Orbigny. (*Dysasterinae*, Gray.)

Apical system disconnected, either elongate or sub-compact. Ambulacra similar; bivium widely separated from the trivium; floscelle absent. Jura to Recent.

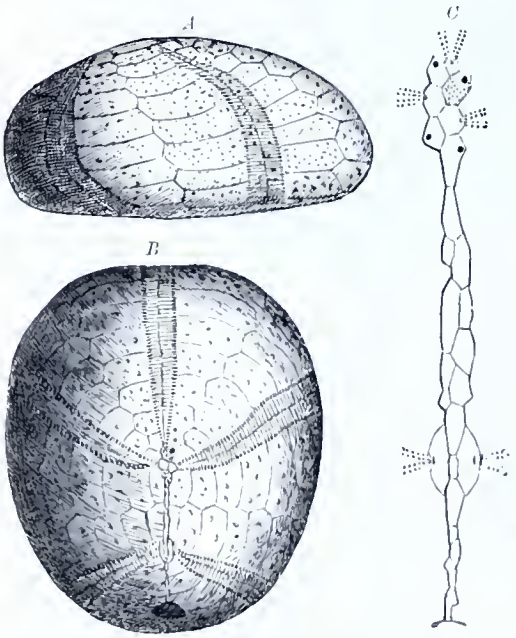

Fig. 390.

Collyrites elliptica, Desm. Callovian; Mamers, Sarthe. *A*, *B*, Test in profile and from above, 1/1. *C*, Dorso-central system, enlarged.

Collyrites, Desm. (Fig. 390). Test ovoid, tumid, more or less truncated posteriorly. *Amb* disjunct, the anterior one sometimes in a slight groove. Width of the *Amb* increasing toward the ambitus; pairs of pores in low primary plates. Periproct posterior, supra-marginal, placed in a groove. Apical system elongate, separated by numerous small plates belonging to the postero-lateral *Amb*. Very abundant in the Middle and Upper Jura and Cretaceous.

Dysaster, Ag. Differs from *Collyrites* in details of the apical system, the basals not being separated by the antero-lateral radial plates. Upper Jura and Lower Cretaceous.

Hyboclypeus, Agassiz. Jura. *Infraclypeus*, Gauthier. Upper Cretaceous. *Grasia*, Mich. Jura.

Metaporhinus, Mich. Test very tall, slightly longer than broad, sub-cordiform, projecting upwards anteriorly, grooved and oblique behind. Anterior

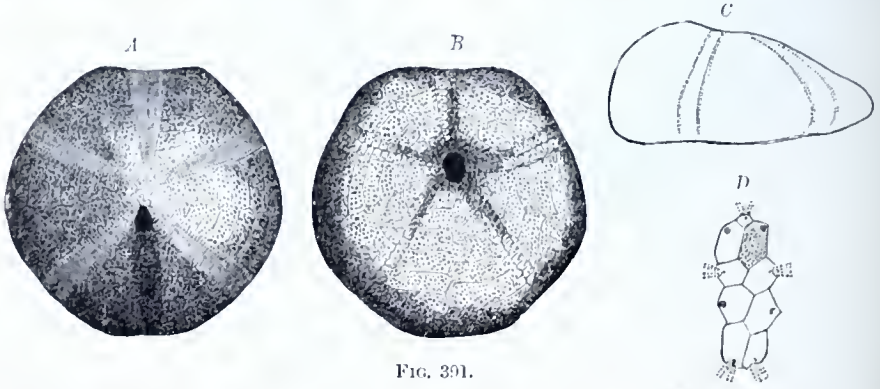

Fig. 391.

Hyboclypeus gibberulus, Ag. Middle Jura; Soleure, Switzerland. *A*, *B*, Dorsal and ventral views. *C*, Profile. *D*, Apical system, enlarged.

Amb in a groove, with small, simple, distant pairs of pores; the other *Amb* flexuous, with comma-shaped pores placed obliquely to one another. Periproct supra-marginal. Upper Jura and Lower Cretaceous.

Sub-Order B. SPATANGOIDEA. Duncan.

Peristome eccentric in front, rarely pentagonal in the adult, usually with a posterior labrum, behind which is a long plastron bounded laterally by the posterior ambulacra. Ambulacra dissimilar. Interambulacra with a single plate at the peristomial margin; the postero-lateral areas usually unsymmetrical actinally. Fascioles present or absent.

Family 1. Ananchytidae. Desor.

Test ovoid or sub-cordiform in marginal outline, tall or depressed, and with large plates. Ambulacra in a bivium and trivium, nearly similar, flush, apetalous; pairs of pores largest near the apex and at the peristome, may be uniporous. Periproct variable in position. Cretaceous to Recent.

Echinocorys, Breyn. (*Ananchytes*, Mercati), (Fig. 392). Test large, oval in marginal outline; high, rounded, or keeled apically, flat actinally. *Amb* biporous, the pairs of pores well developed abactinally, but becoming smaller, closer, and oblique toward the ambitus, where they are more distant. Posterior *Amb* actinally long and broad, the pairs small, and pores oblique. Peristome oval, broader than long. Periproct infra-marginal, posterior, oval. Apical system elongate. Very abundant in the Upper Cretaceous. *E. ovata*, Leske sp., often attains a very large size.

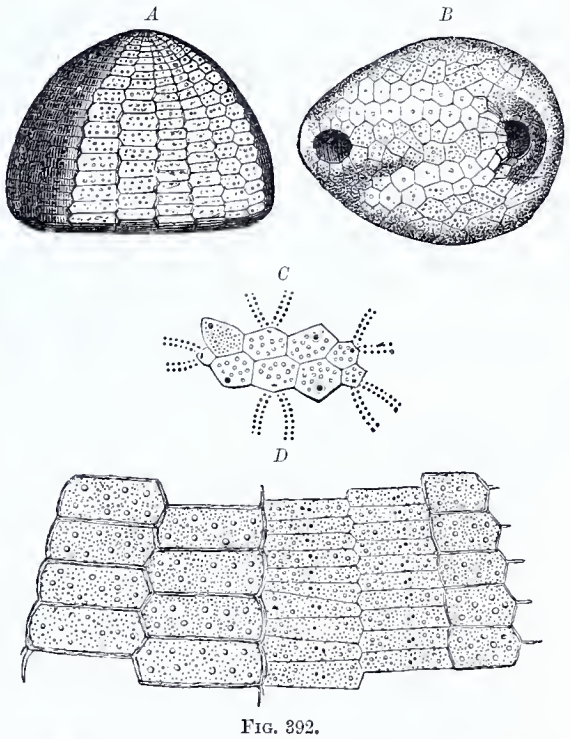

Fig. 392.

Echinocorys ovata, Leske sp. White chalk; Haldem, Westphalia. *A*, *B*, Profile and ventral view, 1/3. *C*, Dorso-central system, enlarged. *D*, Portion of *Amb* and *1Amb* areas, 1/1.

Holaster, Ag. (Fig. 393). Test ovoid in marginal outline, flat actinally, tumid and high abactinally. Anterior *Amb* in a shallow groove. Peristome elliptical, broadest transversely. Periproct supra-marginal, oval. Apical system elongate. Cretaceous and Miocene.

Offaster, Desor. Test small, tumid. Anterior *Amb* sometimes in a shallow groove. Peristome oval, broadest transversely. Periproct supra-marginal, circular or ovoid. Apical system elongate. Cretaceous. *O. pilula*, Ag. sp.

Hemipneustes, Ag. Test large, ovoid in marginal outline, high and tumid dorsally, flat actinally. Anterior *Amb* in a deep, narrow groove extending to

the elongate apical system, its pairs of pores numerous and small, the rows wide apart. Paired *Amb* more or less curved, open distally, with dissimilar

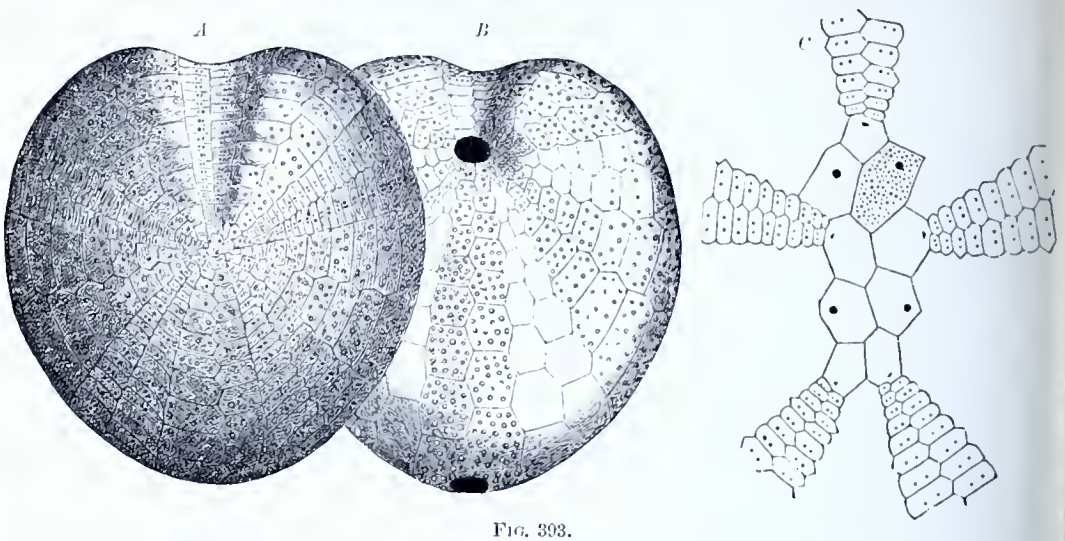

Fig. 393.

A, *B*, *Holaster subglobosus*, Ag. Cenomanian; Rouen. 1/1. *C*, *H. suborbicularis*, Defr. Dorso-central system, enlarged.

pores. Peristome much sunken, crescent-shaped, broad. Periproct supramarginal. Upper Cretaceous. *H. radiatus*, Lam. sp.

Cardiaster, Forbes (*Stegaster*, Pomel, p.p.) Similar to *Holaster*, but anterior groove deeper and with angular margin. Periproct oval, placed in a depression in the truncated posterior face. A more or less complete marginal fasciole passing below the periproct. Cretaceous.

Sub-genus *Infulaster*, Hagw. Test high in front, narrow; anterior groove deep and with strong lateral keels. Fasciole absent. Upper Cretaceous.

Hagenowia, Duncan (*Cardiaster*, Forbes, p.p.; *Stegaster*, Pomel, p.p.) Upper Cretaceous.

Urechinus, *Cystechinus*, A. Ag. Late Tertiary and Recent. *Calymne*, Wyv. Thoms. Recent. *Enichaster*, de Loriol. Oligocene. All with uniporous *Amb*.

Stenonia, Desor. Like *Echinocorys* (*Ananchytes*), except that the apical system is compact, and the *Amb* equal. The solitary species, *S. tuberculata*, Defr. sp., is abundant in the Upper Cretaceous (Scaglia) of the Southern Alps and the Apennines.

Family 2. **Spatangidae.** Wright.

Test ovoid or cordiform, longer than broad, with numerous plates, and usually with an anterior groove. Ambulacra in a bivium and trivium, the anterior differing from the others in shape and construction. Pairs of pores of the petaloid parts differing from the others. Fascioles present or absent. Cretaceous to Recent.

Section A. Adetes. *All fascioles absent.*

Isaster, Desor. Petals not closed. Peristome large, with a posterior labrum. Cretaceons.

Epiaster, d'Orb. (*Macraster*, Roemer.) Anterior *Amb* in a groove; paired

Amb petaloid dorsally, with elongate, unequal pores. *IAmb* tumid dorsally. Peristome transverse, tumid in front, and usually with projecting labrum. Periproct longitudinal, supra-marginal. Cretaceous.

Echinospatagus, Breyn. (*Toxaster*, Ag. p.p.) Anterior *Amb* in a broad shallow groove, with unequal pairs of pores. Paired *Amb* sub-petaloid, flexuous, with unequal poriferous zones and unequal pairs of pores. Peristome transverse, sub-circular, or pentagonal. Tubercles small, perforate, and crenulate. Abundant in Lower and Middle Cretaceous.

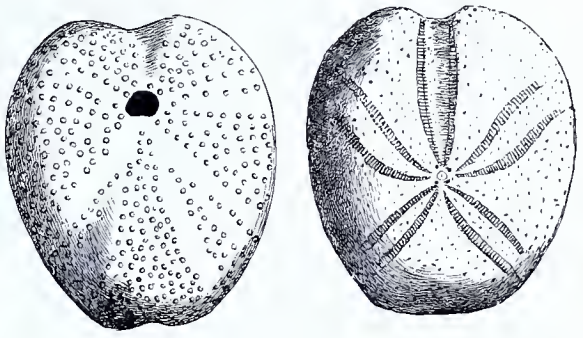

Fig. 394.

Echinospatagus (*Toxaster*) *complanatus*, Ag. Neocomian; Auxerre, Yonne. 1/1.

Ennalaster, d'Orb. (*Heteraster*, d'Orb.) Petaloid parts of antero-lateral *Amb* divergent, flexuous, tending to close, and with very unequal poriferous zones, of which the posterior are the largest; pairs of pores oblique. Postero-lateral *Amb* short, divergent. Peristome labiate, wide, arched in front. Periproct in posterior truncation. Cretaceous.

Hemipatagus, Desor (Fig. 395). Test small, cordiform. Anterior *Amb* with small pores in a shallow furrow. Paired *Amb* long, petaloid, nearly

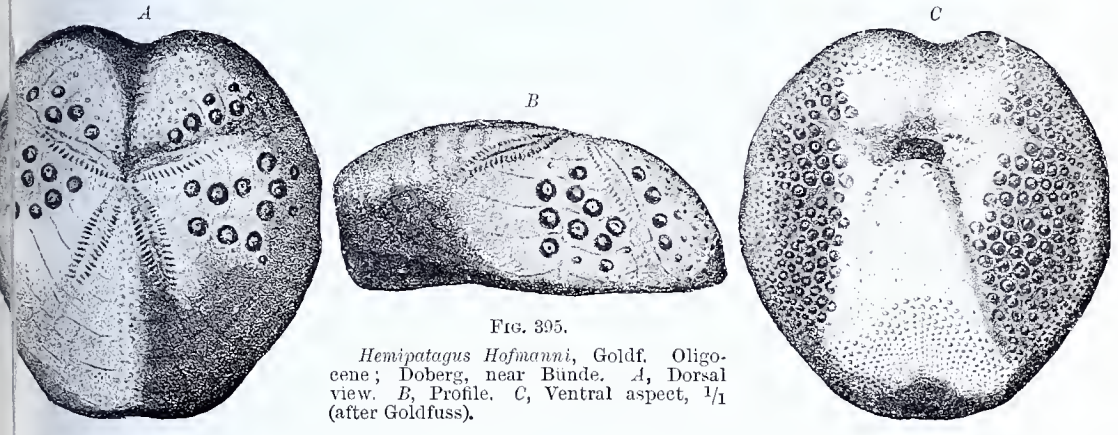

Fig. 395.

Hemipatagus Hofmanni, Goldf. Oligocene; Doberg, near Bünde. *A*, Dorsal view. *B*, Profile. *C*, Ventral aspect, 1/1 (after Goldfuss).

flush. The lateral *IAmb* with a few large perforate and crenulate tubercles in deep scrobicules. Periproct supra-marginal. Tertiary.

Platybrissus, Grube. Recent. *Palaeopneustes*, A. Ag. Recent, and perhaps Eocene.

Section B. Prymnadetes. *Subanal fasciole absent, other fascioles present.*

Hemiaster, Desor (Fig. 396). Anterior *Amb* in a shallow groove, the pores oblique, and in pairs on either side. Antero-lateral *Amb* petaloid dorsally, sunken, diverging, and much longer than the postero-lateral. Pores of the petaloid parts conjugated, the outer ones usually the largest. Peripetalous fasciole present.

Sub-genus *Tripylus*, Phill. (*Abatus*, Troschel). Recent.

Faorina, Gray. Recent. *Pericosmus*, Ag. Cretaceous and Tertiary.

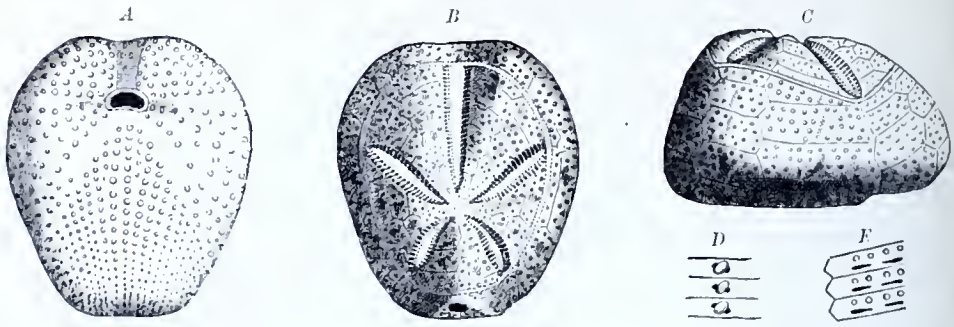

FIG. 396.

Hemiaster Orbignyanus, Desor. Upper Cretaceous; Martigues, Provence (after d'Orbigny). *A-C*, Ventral, dorsal and side views of test, 1/1. *D*, Pores of the odd *Amb*. *E*, Pores of the paired *Amb*, enlarged.

Linthia, Merian (*Desoria*, Gray), (Fig. 397). Anterior *Amb* in a deep

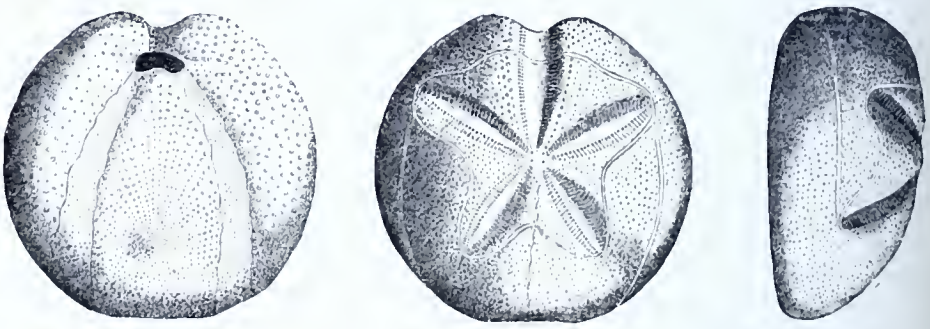

FIG. 397.

Linthia Heberti, Cotteau. Eocene; Lonigo, near Vicenza. 3/4 natural size (after Dames).

groove, the pores round and small, in pairs on either side. Antero-lateral *Amb* longer and more divergent than the others, with petals sunk in grooves. Pores conjugated. A peripetalous and lateral fasciole present. Cretaceous to Recent.

Schizaster, Ag. (Figs. 398, 399). Resembling *Linthia*, but the apical system posteriorly eccentric, and the *Amb* very diverse. Tertiary and Recent.

Prenaster, Desor; *Ornithaster*, *Coraster*, Cotteau. Eocene.

Agassizia, Val.; *Moira*, A. Ag. Tertiary and Recent. *Moiropsis*, A. Ag. Recent.

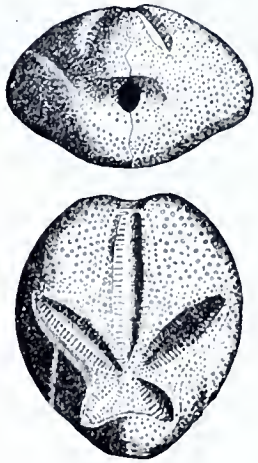

FIG. 398.

Schizaster Archiaci, Cott. Eocene; San Giovanni Ilarione, near Vicenza.

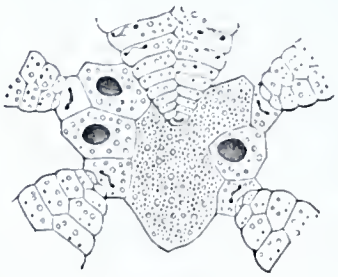

FIG. 399.

Schizaster fragilis, Ag. Apical system, greatly enlarged (after Lovén).

SECTION C. PRYMNODESMIA.
Subanal fasciole present.

Micraster, Ag. (Figs. 400, 401). Test cordiform, tumid, rather depressed. Anterior *Amb* apetaloid, in a shallow depression; antero-lateral *Amb* sub-petaloid dorsally, diverging;

postero-lateral shorter than the others, with elongate, conjugated pores. Periproct supra-marginal; apical system eccentric in front. Broad subanal fasciole. Abundant in Middle and Upper Cretaceous; less common in Eocene and Miocene.

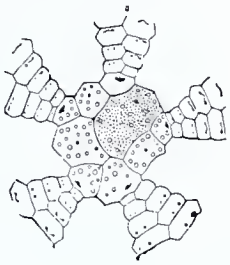

Fig. 400.
Micraster coranganium, Lam. Apical system.

Brissus, Klein (*Brissomorpha*, Laube); *Meoma*, Gray; *Metalia*, Gray. Tertiary and Recent. *Rhinobrissus*, A. Ag. Recent.

Brissopsis, Ag. (*Deakia*, Pavay), (Fig. 402). *Amb* unequal, bare and large near the peristome. Anterior *Amb* slightly sunken, with small pairs of close pores. Paired *Amb* sunken, the antero-lateral pair sub-petaloid, equal to or larger than the postero-lateral, straight or curved. A subanal and peripetalous fasciole. Tertiary and Recent.

Sub-genus *Cyclaster*, Cotteau. Antero-lateral *Amb* divergent. Eocene.

Brissopatagus, Cotteau. Allied to *Brissopsis*. Eocene.

Spatangus, Klein. Anterior *Amb* in a broad, deep groove, with distant pairs of small pores. Paired *Amb* petaloid, with broad, sunken poriferous zones. Periproct large, supra-marginal, transverse. *IAmb* with large crenulate and perforate primary tubercles, and fine granulation. Subanal fasciole only. Tertiary and Recent.

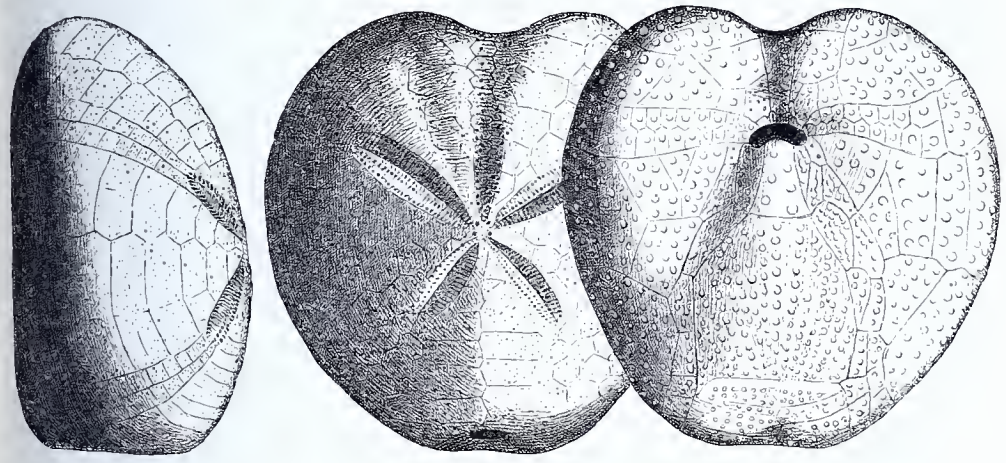

Fig. 401.
Micraster cortestudinarium, Goldf. White Chalk; Meudon, near Paris. Natural size.

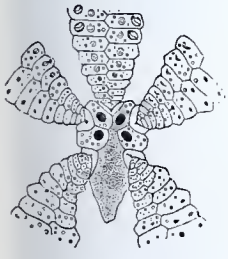

Fig. 402.
Brissopsis lyrifera, Forbes. Apical system, enlarged (after Lovén).

Maretia, Gray. Tertiary and Recent.

Eupatagus, Ag. Anterior *Amb* in a shallow, abactinal depression, narrow, and with small, distant pairs of pores. The paired *Amb* petaloid dorsally, long, wide, closed; poriferous zones broad, more or less sunken; pores dissimilar. Peripetalous and subanal fasciole. Tertiary and recent.

Sub-genus *Macropneustes*, Ag. (*Peripneustes*, Cott.), (Fig. 402 *bis*). Test large, thick, cordiform. Petals elongate or broad, grooved or semi-flush, open or imperfectly closed. Poriferous zones of equal width with the interporiferous. Eocene and Recent.

Gualtieria, Desor. Eocene. *Echinocardium*, Gray; *Breynia*, Desor; *Lovenia*, Ag. and Desor. Tertiary and Recent.

Section D. Apetala.

Ambulacra flush, apetalous, generally uniporous, and either similar or diverse; plates high, few, often hexagonal. Fascioles usually present.

Under this head are included the following recent genera, all but the first two of which have fascioles:—*Genicopatagus*, *Palaeobrissus*, A. Ag.; *Aceste*, Wyv. Thomson; *Aërope*, Norman; *Palaeotropus*, Lovén; *Homolampas*, *Argopatagus*, A. Ag.; and *Cleistechinus*, de Loriol. Miocene.

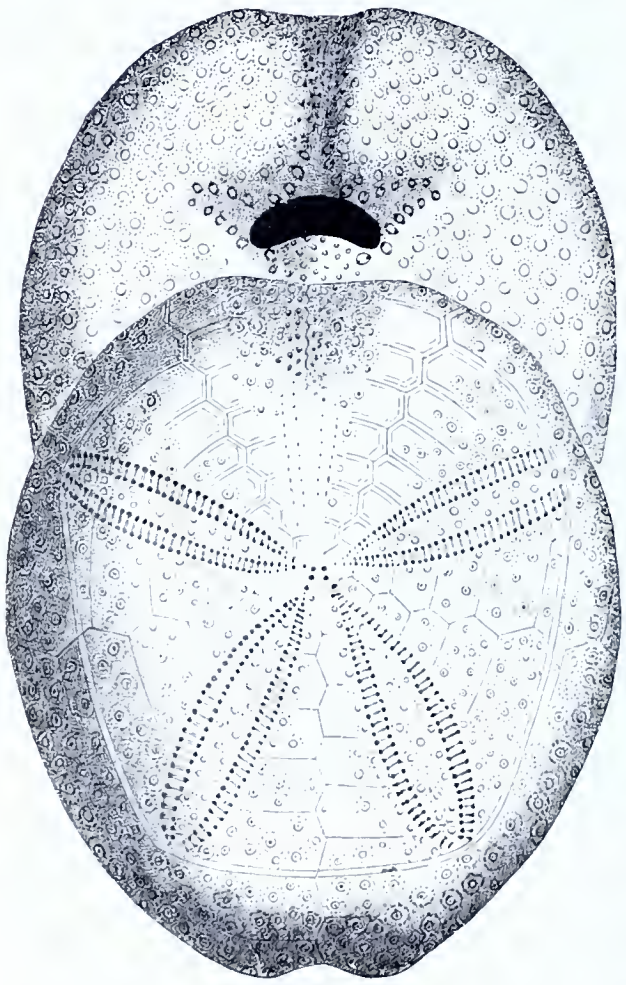

Fig. 402 *bis.*

Macropneustes Meneghinii, Desor. Eocene; Monte Spiado, near Vicenza.

Family 3. **Leskiidae**. Gray.

Test thin, ovoid. Apical system with three basal plates fused into one. Peristome eccentric in front, pentagonal, with five angular buccal plates.

Palaeostoma, Lovén (*Leskia*, Gray). Recent; China, East Indian Islands.

Family 4. **Pourtalesiidae**. Lovén.

Test very elongate, subcylindrical or obconical, truncated anteriorly, flat actinally. Peristome in a deep anterior recess; periproct actinal, or above the projecting posterior rostrum when such is present. Ambulacra flush, apetalous, sometimes discontinuous; pores single or slit-like.

Pourtalesia, *Spatagocystis*, *Echinocrepis*, A. Ag. Recent.

Range and Distribution of the Echinoidea.

Fossil Sea-Urchins make their appearance as early as the Ordovician, but are represented very sparsely by forms differing in a marked degree from the normal (*Bothriocidaris*, *Echinocystites*). The order *Perischoëchinoida*, characterised by its supernumerary columns of plates, is widely, but by no means numerously, distributed in the Devonian and Carboniferous of North America and Europe.

Fragmentary remains of true Cidarids are found in the Permian, perhaps

even in the Carboniferous (*Eocidaris*), but not until the Mesozoic era do the *Euechinoidea* completely replace the *Palæechinoidea*, which become extinct with the Triassic *Tiarechinus*.

All of the Triassic *Euechinoidea* are true Cidarids, and occur chiefly in the Alps. Some of them are remarkable for their massive spines, which are found in places, as at St. Cassian, very profusely ; perfect tests, however, are rare. The European Lias yields a few Cidarids, and also the oldest known exocyclic Urchins (*Galeropygus*, *Pygaster*).

Especially rich in regular Sea-Urchins, as well as in members of the *Echinoneidae*, *Cassidulidae*, and *Collyritidae* are the Middle and Upper Jura of England, France, Germany, Switzerland, the Alps, and Northern Africa. The Lower Cretaceous of the same region exhibits no essential change in the Echinoid fauna ; but the advent of large numbers of the *Ananchytidae* and *Spatangidae* in the Middle and Upper Cretaceous of Europe, Northern Africa, Asia, and North America imparts to these horizons a characteristic appearance.

During the Tertiary the *Cidaridae* notably decline, the *Echinoconinae* become entirely extinct, and the Clypeastroids and Spatangoids advance conspicuously into the foreground, taking on more and more the semblance of recent species. Tertiary Sea-Urchins are distributed over the whole world, and are particularly plentiful in the Nummulitic Limestone of Europe, Northern Africa, Asia Minor, and India.

As to phylogenetic relationships, the *Perischoëchinoida* may very properly be regarded as the forerunners and ancestors of the regular *Euechinoidea*. Among the latter the *Cidaridae* form the most primitive and stable type ; the *Diadematoida*, on the other hand, exhibit a much greater aptitude for variation.

Whether the irregular *Euechinoidea* are to be regarded as derived from the Silurian *Echinocystites*, or from the regular *Euechinoidea*, is an open question. It is obvious, however, that the gnathostomous *Echinoconidae* are in a number of respects very closely related to the *Regulares*. The atrophy of teeth in the *Echinoneidae* certainly gave rise to the *Cassidulidae*, and subsequent modifications led to the derivation of the *Ananchytidae* and *Spatangidae*. The Clypeastroids may also be looked upon with much plausibility as a peculiarly modified offshoot of the *Echinoconinae*, and also as having affinities with the Holectypoid genus *Discoidea*. The parallelism between ontogeny and phylogeny as manifested in various groups of the *Echinoidea* is very striking.

Class 2. HOLOTHURIOIDEA. Forbes.

The Holothurians, or Sea-Cucumbers, differ markedly from all other Echinoderms, being characterised by the possession of an elongated, vermiform body, a terminal anus, and contractile tentacles surrounding the mouth, and by the absence of a test proper.

Their palaeontological importance is small, since the only structures they possess which are at all capable of preservation are the small integumentary calcifications, occurring in the form of wheels, spicules, spherules, anchors, etc. Such detached calcareous structures are known from the British Carboniferous rocks, from the Lias and Dogger of Lorraine, the Upper Jura of Franconia, and the Cretaceous of Bohemia ; they are unquestionably of Holo-

thurian origin, but as a rule are incapable of more precise determination. On the other hand, however, Schlumberger has described a number of minute calcareous bodies from the Calcaire Grossier (Eocene) of Paris, which seem very certainly referable to the genera *Synapta*, *Chirodota*, and *Myriotrochus*.

TABLE SHOWING THE VERTICAL RANGE OF THE ECHINOIDEA.

Families.	Ordovician.	Silurian.	Devonian.	Carboniferous.	Permian.	Trias.	Jura.	Cretaceous.	Tertiary.	Recent.
I. Palæechinoidea										
Order 1. *Cystocidaroida*		—								
,, 2. *Bothriocidaroida*	—									
,, 3. *Perischoëchinoida*		—	—	—	—	—				
II. Euechinoidea										
Order 1. *Cidaroida*										
1. Cidaridae				?	—	—	—	—	—	—
Order 2. *Diadematoida*										
1. Echinothuridae							—	—		—
2. Saleniidae							—	—	—	—
3. Hemicidaridae					—	—	—	—	—	—
4. Diadematidae							—	—	—	—
5. Cyphosomatidae							—	—	—	—
6. Arbaciidae									—	—
7. Temnopleuridae								—	—	—
8. Echinometridae									—	—
9. Echinidae								—	—	—
Order 3. *Holectypoida*							—	—	—	—
,, 4. *Clypeastroida*										
1. Fibulariidae								—	—	—
2. Clypeastridae									—	—
3. Scutellidae									—	—
Order 5. *Spatangoida*										
1. Echinoneidae								—	—	—
2. Cassidulidae							—	—	—	—
3. Collyritidae							—	—	—	—
4. Ananchytidae								—	—	—
5. Spatangidae								—	—	—
6. Leskiidae										—
7. Pourtalesiidae										—

Sub-Kingdom IV. VERMES. Worms.[1]

Bilaterally symmetrical animals with unsegmented or uniformly segmented, and usually elongated, bodies. Segmented lateral appendages wanting. A dermal muscular system and paired excretory canals (water-vascular system) present.

Of all the larger divisions of the animal kingdom, none is so poorly adapted for preservation in the fossil state as the Worms, whose bodies, as a rule, are totally without hard parts.

All Worms are laterally symmetrical, and in every case a dorsal and ventral surface is distinguishable. The group of unsegmented Worms (*Vermes* proper, as restricted by some authors) have either flat or cylindrical bodies, and are accordingly distinguished as *Platyhelminthes* or Flat Worms, and *Nemathelminthes* or Round Worms. But with the exception of a few rare parasitic forms discovered in Carboniferous insects, or in insects enclosed in amber, neither of these classes is represented in the fossil state.

The segmented Worms, or *Annelida*, are characterised by a division of the body into metameres, which, although primitively alike, do not always remain homonomous. They have a brain, a circumoesophageal ring, a ventral chain of ganglia, and a vascular system. The body is more or less elongated, and sometimes flattened, sometimes cylindrical. According as the internal segments correspond exactly with the external, or as each internal segment corresponds to a definite number (3, 4, or 5) of the external rings, two

[1] Literature :

Pander, C. H., Monographie der fossilen Fische des silurischen Systems des russisch-baltischen Gouvernements, 1851.

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Ehlers, E., Ueber fossile Würmer aus dem lithographischen Schiefer in Bayern (Palaeontographica, Bd. XVII.), 1868.

Claparède, E., Recherches sur la structure des Annélides sédentaires, 1873.

Newberry, J. S., Palaeontology of Ohio, vol. II. part 2, 1875.

Hinde, G. J., On Conodonts from the Chazy and Cincinnati Groups ; and on Annelid Jaws from the Cambro-Silurian, Silurian, and Devonian Formations in Canada, and from the Lower Carboniferous in Scotland (Quar. Journ. Geol. Soc., vol. XXXV.), 1879.

Hinde, G. J., On Annelid Jaws from the Wenlock and Ludlow Formations of the West of England (Quar. Journ. Geol. Soc., vol. XXXVI.), 1880.

Etheridge, R., jun., British Carboniferous Tubicolar Annelides (Geol. Mag.), 1880.

Nathorst, A. G., On the Tracks of some Invertebrate Animals and their Palaeontological Significance (K. Svensk. Vetensk. Akad. Handl., Bd. XVIII., XXI.), 1881-86.

Hinde, G. J., On Annelid Remains from the Silurian Strata of the Isle of Gotland (Bihang till K. Svensk. Vetensk. Akad. Handl., Bd. VII.), 1882.

Zittel, K. A., and *Rohon, J. V.*, Ueber Conodonten (Sitzungsber. Bay. Akad. Wissensch., Bd. XVI.), 1886.

Clarke, J. M., Annelid Teeth from the Lower Portion of the Hamilton Group, New York (Sixth Annual Report State Geologist, 1886).

sub-classes are distinguished, *Chaetopoda* and *Hirudinea*. A further difference is to be noticed in the locomotive organs, the *Chaetopoda* having bristle-bearing, unjointed appendages (*parapodia*) on each ring of the body; and the *Hirudinea* having a terminal sucker. The latter group includes only the Leeches, which are not known with certainty in the fossil state.

It is only the one order of marine Worms (*Polychaeta*) belonging to the sub-class *Chaetopoda* with which the palaeontologist is practically concerned; as the Earthworms and their allies (*Oligochaeta*) are wholly unknown as fossils. The marine *Chaetopoda* are divisible into two principal sections, known as the Sedentary or Tubicolous Worms, and the Nereid or Errant Annelides.

Sub-Order A. TUBICOLA. (Sedentaria.)

Polychaetous Annelides with indistinctly separated head, and short, usually non-protrusible proboscis, without jaws. Parapodia short, and never used for swimming. Inhabiting more or less firm tubes, which they construct for themselves, and subsisting upon vegetable matter.

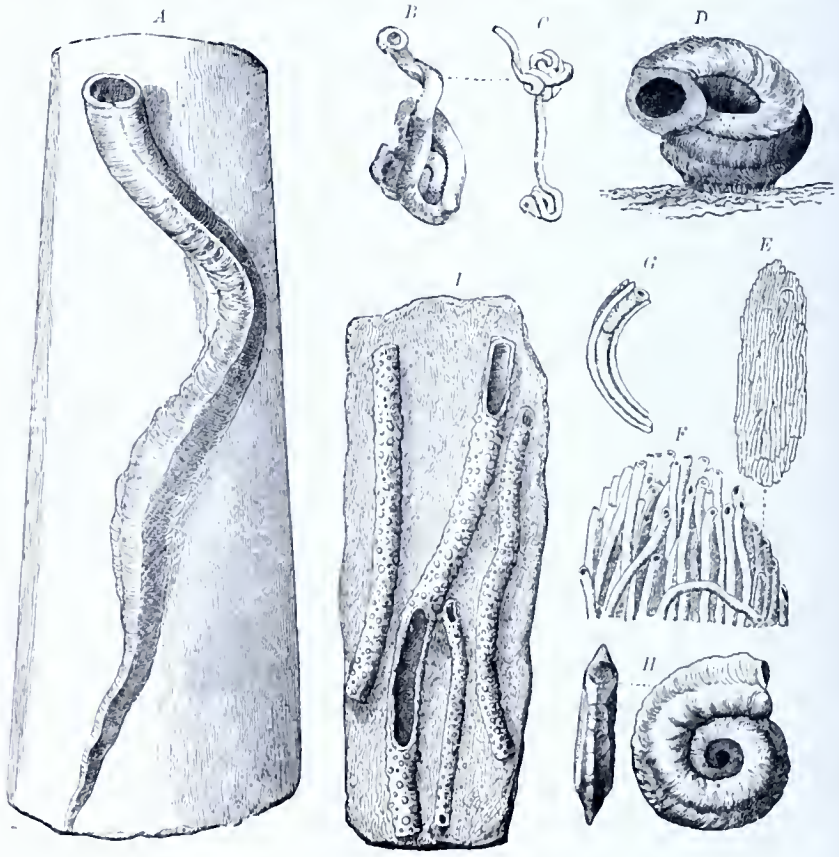

FIG. 403.

A, *Serpula limax*, Goldf. Middle Jura; Franconia. *B*, *C*, *S. gordialis*, Schloth. Upper Cretaceous: Bannewitz, near Dresden. *D*, *S. convoluta*, Goldf. Middle Jura; Stuifen, Wurtemberg. *E*, *S. socialis*, Goldf. Middle Jura; Lahr, Baden. *F*, Same, enlarged. *G*, *S. septemsulcata*, Reich. Upper Cretaceous; Bannewitz. *H*, *S.* (*Rotularia*, Defr.) *spirulaea*, Lam. Eocene; Monte Berici, near Vicenza. *I*, *Terebella lapilloides*, Münst. Upper Jura; Streitberg, Franconia.

The Tubicolous Annelides invest themselves with a protective tube of usually irregular form, to which they are not organically connected, and in

which they can move freely. Sometimes the tubes are free, but more commonly they are attached to foreign objects, either by the apex or by one side, and may occur either singly or in clusters. The tubes frequently consist of concentric layers of lime-carbonate, with vesicular cavities between the lamellae, or the latter may be traversed by fine tubuli. In other cases the tubes are composed of agglutinated grains of sand and other foreign particles; or they may be membranaceous or leathery. The materials for constructing the tubes are procured by the tentacles or branchial filaments of the head, and are cemented together by a glutinous secretion from large glands. Fossil worm-tubes are by no means of infrequent occurrence, and are known from rocks as old as the Ordovician. Only a few of the more common examples can be mentioned here.

Serpula, Lin. (Fig. 403). Under this head are included the majority of fossil Tubicolar Annelides. They build firm, irregularly contorted, sometimes spirally enrolled, free or adherent calcareous tubes, which are frequently clustered together in large numbers. Beginning in the Silurian, they are sparsely represented in the Palaeozoic era; but from the Jura onward, numerous forms are met with, the usual condition being parasitic upon other fossils. Notably in the Lower Cretaceous their gregarious masses form beds of considerable thickness (Serpulitenkalk of Braunschweig, Serpulitensand of Bannewitz, near Dresden). *S. spirulaea*, Lam. (Fig. 403 *H*) is an abundant and characteristic Eocene species. Living Serpulas have a world-wide distribution.

Terebella, Cuv. (Fig. 403 *I*). Cylindrical, elongate, more or less bent tubes, composed of cemented grains of sand or other adventitious particles. Lias to Recent.

Spirorbis, Daudin (*Microconchus*, Murch.), (Fig. 404). Minute, snail-like, or spirally enrolled calcareous tubes, cemented by the flat under side. The spiral may be either dextral or sinistral, and is usually ornamented externally with concentric striae or annulations, sometimes with tubercles or spines. Abundant in the Palaeozoic formations from the Ordovician onward, and also at the present day; somewhat less common in the Mesozoic and Cenozoic eras. Living species usually adherent on seaweeds.

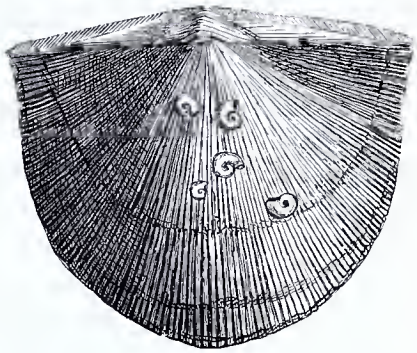

FIG. 404.

Spirorbis omphalodes, Goldf. sp. Tubes attached to a Brachiopod shell (*Orthothetes umbraculum*). Devonian; Gerolstein, Eifel.

The following genera are commonly regarded as Annelides, but their position is doubtful:—

Serpulites, Murch. Very long, smooth, compressed, and somewhat bent calcareous tubes, the layers admixed with organic substance. Silurian.

Cornulites, Schloth. Thick-walled, trumpet-shaped tubes, closed at the lower end, and sometimes attaining a length of three or four inches. Exterior annulated, and covered with very fine longitudinal striae. Ordovician to Devonian.

Ortonia, Nich. Small, conical, slightly flexuous, thick-walled calcareous tubes, cemented by the whole of one surface to some foreign body. Sides of

the tube ringed with imbricating annulations, the free upper surface apparently cellular in structure. Ordovician to Carboniferous.

Conchicolites, Nich. Conical, slightly bent, thin-walled tubes, growing together in clusters, and attached by the small lower ends to Orthoceras or Brachiopod shells. Tubes made up of numerous short rings, each of which partially overlaps the one below. Ordovician.

Sub-Order B. ERRANTIA. (Nereidae.)

Free-swimming, predaceous Polychaeta, with well-marked head. Proboscis capable of protrusion, and armed with papillae or powerful jaws. Parapodia much more developed than in the Tubicola, beset with setae, and serving for locomotion.

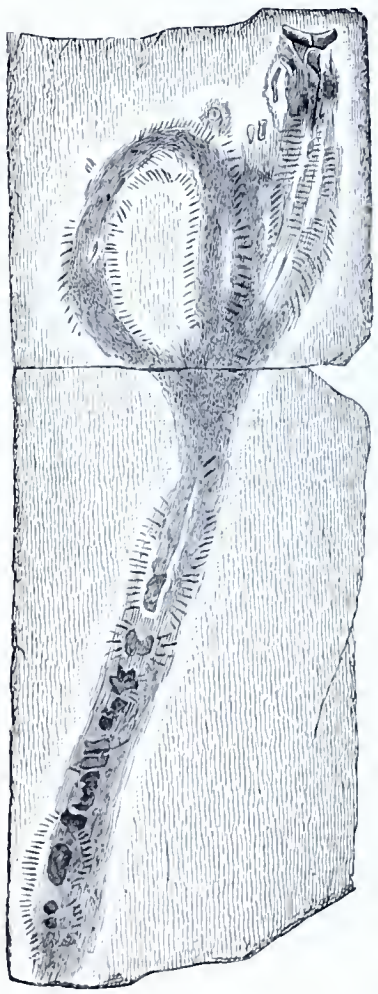

Fig. 405.

Eunicites avitus, Ehlers. Lithographic Slates; Eichstadt, Bavaria. Natural size.

Undoubted remains of Errant Worms have long been known from the Lithographic Slates (Upper Jura) of Bavaria, and include the trails, calcified jaws, and excrements of numerous species. The principal genus from this horizon is *Eunicites*, Ehlers (*Geophilus*, Germar), (Fig. 405), perfect impressions of which are also found in the Eocene shales of Monte Bolca.

Under the head of *Lumbricaria*, Münster (*Lumbricites*, Schlotheim), (Fig. 406), are included a variety of obscure remains from the Lithographic Slates, which may be best regarded as the excrements of Annelides. They occur as irregularly contorted bands or strings, sometimes in the form of labyrinthic coils, and are usually of considerable length.

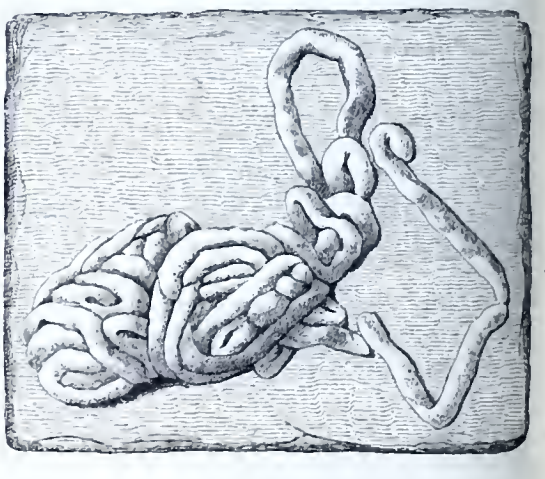

Fig. 406.

Lumbricaria colon, Münst. Lithographic Slates; Solenhofen, Bavaria. Natural size.

The *Myzostomidae*, which are parasitic on living Comatulas, are shown by Graff to have infested also the column segments of Jurassic Crinoids.

Of peculiar interest are the minute detached jaws and toothed plates discovered by Hinde in the Ordovician, Silurian, Devonian, and Carboniferous rocks of Canada, Great Britain, and Sweden (Island of Gottland). These are

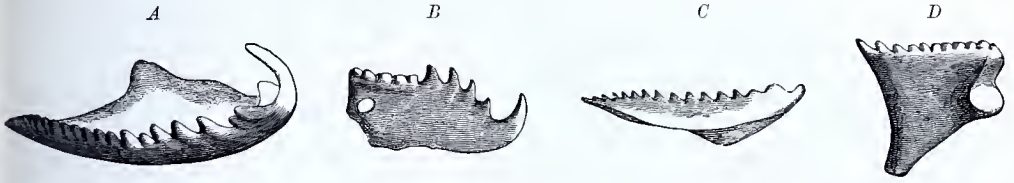

FIG. 407.

Palaeozoic Annelide-jaws. *A*, *Lumbriconereites basalis*, Hinde. Silurian; Dundas, Ontario. $^{10}/_{1}$. *B*, *Oenonites rostratus*, Hinde. Toronto. $^{15}/_{1}$. *C*, *Eunicites varians*, Grinnell. Toronto. $^{6}/_{1}$. *D*, *Arabellites scutellatus*, Hinde. Ordovician; Toronto. $^{16}/_{1}$.

very small, black, highly lustrous bodies, extremely variable in form (Fig. 407), and mainly composed of chitinous material which is unaffected by acid.

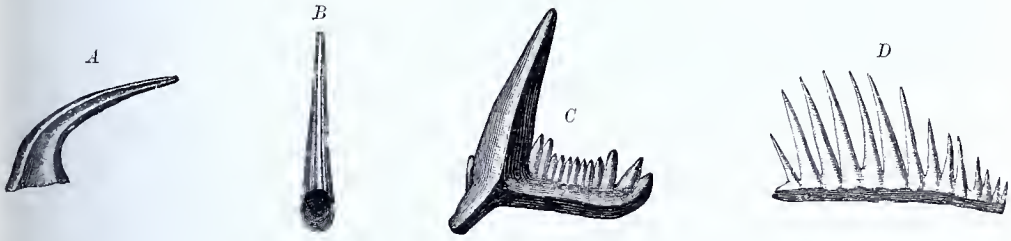

FIG. 408.

Conodonts, highly magnified. *A*, *B*, *Paltodus truncatus*, Pand. (after Pander). *C*, *Prioniodus elegans*, Pand. Cambrian; St. Petersburg. *D*, *Polygnathus dubius*, Hinde. Devonian; North Evans, New York. $^{20}/_{1}$.

They exhibit a striking resemblance to the jaws of recent Annelides, and probably represent a large number of genera.

Of less certain derivation are the microscopic teeth so well described by Pander under the name of "Conodonts" (Fig. 408), which occur detached in the Cambrian (Blue Clay underlying the Ungulite Grit) of St. Petersburg, and are also very abundant in beds of Ordovician, Silurian, and Carboniferous age in Russia, Great Britain, the United States, and Canada. They are usually translucent, of a shiny, reddish horn-colour, and are composed of carbonate and phosphate of lime. They, too, exhibit great variety in form. By Pander and others these fossils have been regarded as fish-teeth. Zittel and Rohon, however, consider that they are Annelid jaws, but their true position cannot yet be said to be satisfactorily determined.

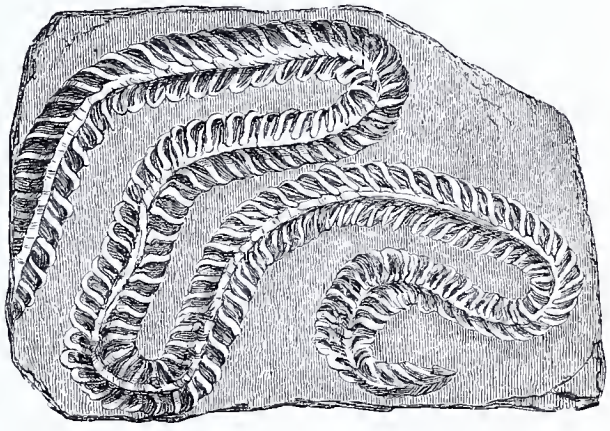

FIG. 409.

Nereites Cambrensis, M'Leay. Cambrian; Llampeter, Wales. Natural size.

A quantity of supposed worm-borings, trails, impressions, and other

obscure remains have been described from the older Palaeozoic formations. The burrows have the form of straight or tortuous tunnels, and are sometimes hollow, but more commonly have been filled up by the matrix of the rock. Various names have been applied to them, such as *Scolithus*, *Arenicola*, *Histioderma*, *Planolites*, *Diplocraterion*, *Spirocolex*, *Scolecoderma*, etc., but they are obviously incapable of precise determination.

Fig. 410.

Crossopodia (*Crossochorda*) *scotica*, M'Coy. Ordovician; Bagnoles, Normandy.

Similarly, the serpentine or vermiform impressions known as *Nereites*, consisting usually of a number of windings, and often of profuse occurrence in various Palaeozoic formations, were until quite recently regarded as worm-tubes, or markings made by Fucoids. These also have received numerous appellations, such as *Nereites* (Fig. 409), *Nemertites*, *Myrianites*, *Nemapodia*, *Crossopodia* (Fig. 410), *Phyllodocites*, *Naites*, etc. Nathorst, however, has brought forward experimental evidence to demonstrate that the majority of these markings have been produced by the movements of Crustaceans, Annelides, and Gastropods. A like origin may be reasonably ascribed to the extraordinarily abundant and variable vermiform structures known as "Hieroglyphics," which occur in the Flysch, Carpathian Sandstone, and in the marine facies of the Cretaceous and Jurassic formations.

Sub-Kingdom V. MOLLUSCOIDEA.

UNDER the term *Molluscoidea*, Milne-Edwards included the *Bryozoa* and *Tunicata*, of which the first had been previously regarded as Zoophytes, and the second as Mollusks. Huxley afterwards assigned the *Brachiopoda* to the same phylum. These three classes form a group intermediate in position between the Worms and Mollusks, and are considered by many zoologists as directly related to the one or the other. The *Tunicata* have more recently been regarded as an independent animal type, and as the probable progenitors of the Vertebrates. To the palaeontologist, however, they are devoid of practical interest, owing to their total lack of hard parts.

The typical *Molluscoidea* either secrete a calcareous shell, or are invested with a membranaceous or corneous covering. The respiratory organs lie anterior to the mouth, and are in the form of tentacles or fleshy spiral appendages. The mouth conducts into a closed alimentary canal. The nervous system is highly organised, and proceeds from a central ganglion, situated in most cases between the mouth and the anus. Reproduction is either sexual or takes place by budding. The ontogeny of the *Molluscoidea* is most nearly comparable with that of the Annelids.

All of the *Molluscoidea* are water inhabitants; the Bryozoans are largely, and the Brachiopods exclusively, marine forms.

Class I. BRYOZOA. Ehrenberg.[1]

Small, almost always composite animals forming by gemmation variously shaped colonies, each zoöid of which is enclosed in a membranaceous or calcareous double-

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walled sac (zoœcium), and possesses typically a freely suspended alimentary canal with mouth and anus. Mouth surrounded by a crown of hollow, slender, ciliated tentacles arranged in the form of a circle or crescent. Usually hermaphrodite.

The *Bryozoa*, or *Polyzoa*, most nearly resemble certain Corals (*Tabulata*) and Hydrozoans in their external configuration, but differ from them radically in the possession of a closed alimentary canal, a highly developed nervous system, and delicate respiratory tentacles surrounding the mouth. With the exception of the solitary genus *Loxosoma*, all Bryozoans live together in colonies or *zoaria*, of greater or lesser extent, and of either calcareous, corneous, or membranaceous composition. These colonies, which are formed by frequently repeated gemmation, present a multitudinous variety of form, habit, and structure. Sometimes they grow into plant-like tufts, composed of a series of cells variously linked together; very commonly they spread over shells and other foreign bodies, forming delicate interwoven threads, crusts of exquisite pattern, or hemispherical, globular, or nodular masses of considerable size; often they rise into branching stems, and fronds of varying width; and at other times the cell-bearing branches form most regular and beautiful open-meshed lace-work.

Each individual is enclosed in a separate chamber (*zoœcium*) of either utricular or more or less tubular form. Occasionally the zoœcia are quite distinct from their neighbours; more commonly, however, intercommunication is effected, either by means of minute "connecting foramina" piercing the chamber walls, or by a common canal to which all the zoöids are attached. A true coenenchyma, such as is found among the Coelenterates, never occurs, and coenenchymal gemmation is accordingly unknown; but a somewhat similar "vesicular tissue" not infrequently occupies the interzoœcial spaces which have resulted from the erection of the zoœcial tubes.

Such vesicular tissue occurs constantly in the *Fistuliporidae* and *Cystodictyonidae*, and in the latter the primary, or even the prostrate cells, are not entirely contiguous. The upper walls of the vesicles, at least, are abundantly perforated; and when with increasing age the vesicles become filled with a secondary deposit, these pores are not obliterated, but continue to pass through such deposits in the form of minute vertical tubes. Precisely the same kind of tissue occurs in other Bryozoans, notably among adult individuals of certain *Fenestellidae*, in which the expanded base of the colony is largely vesicular, and the fenestrules and spaces between the carinae of the branches are filled with vesicles for some distance up. The real purpose of this tissue is to support the zoœcia and to strengthen the zoarium.

However diverse the external aspect of the composite structure, the small builders themselves conform to a simple and quite definite type. Briefly, the animal consists of an alimentary canal, in which three distinct regions, an oesophagus, stomach, and intestine, are recognisable. This is enclosed in a sac, and so bent upon itself that its two extremities, or openings, approximate; one of them, the oral, being either entirely or partially surrounded by a row of slender, hollow, and ciliated tentacles, which serve for respiration and for sweeping food toward the mouth. In most cases the anal opening is situated without the ring of tentacles (*Ectoprocta*), rarely within the same (*Entoprocta*). Heart and vascular system are wanting, but a nervous ganglion, sending

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Pergens, E., Revision des Bryozoaires du Cretacé, etc. (Bull. Soc. Belge Geol., III.-VI.), 1889-92.
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Ulrich, E. O., Lower Silurian Bryozoa (Geol. Survey Minnesota, Final Report, vol. III.), 1892.

out delicate nerve filaments to the tentacles and oesophagus, lies between the mouth and anus. The upper or anterior part of the sac is generally flexible and admits of being invaginated by the action of numerous, longitudinal, and transverse muscles, which traverse the fluid-filled visceral cavity.

Reproductive organs are developed in various parts of the cavity, the spermatozoa usually in the lower, the ova in the upper portion. The ova may be developed in a special receptacle (*marsupium*) attached to the zoœcium, or in an inflation of the surface of the zoarium (*gonocyst*); in other cases, a modified zoœcium (*gonoecium*) is set apart for reproductive functions. The general term *œcium* or *ovicell* is applicable to all of these structures.

Many Bryozoans are provided with appendicular organs known as *avicularia* and *vibracula* (Fig. 411). Their functions are somewhat doubtful, some authors regarding them as food-procuring agents, and others as organs of defence. The avicularia may be immovably attached to the zoœcium; but, as a rule, especially among recent forms, they are pedunculate, and capable of considerable swaying motion. Often, as in *Bugula* and *Bicellaria*, they resemble the head of a bird, consisting of a helmet-shaped upper piece, with a formidable hooked beak, and a mandible worked by powerful muscles. The jaws open and close with a perpetual snapping motion, and small organisms or other foreign particles happening in their way are seized and held with a tenacious grasp. The vibracula are flexible, bristle-like appendages, generally set in the excavated summit of a knob-like elevation, or on a blunt spine.

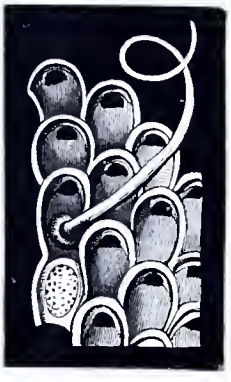


Fig. 411.

Selenaria maculata, Busk. Recent. Enlarged portion of upper surface showing a vibraculum and ovicell (after Busk).

The avicularia and vibracula are themselves incapable of preservation, but their former presence on fossil specimens may be generally determined by the slight pore-like excavations in which they were lodged. The tubular spines, or *acanthopores*, which are of such common occurrence in Palaeozoic Bryozoans, were, in part at least, probably the supports of similar structures.

The term *lunarium* is applied to a more or less thickened portion of the posterior wall in many Palaeozoic Bryozoans, which is curved to a shorter radius and usually projects above the plane of the zoœcial aperture. *Mesopores* are angular or irregular cells occupying interzoœcial spaces in certain Palaeozoic genera.

Most Bryozoans are attached, either by the greater part of their surface, or only basally, to extraneous objects; or they are moored to the bottom by root-like appendages. In many forms the zoarium is regularly jointed. The majority of genera inhabit the sea, and occur in all zones and at all depths; only a few genera live in fresh water. The animals subsist chiefly on Diatoms, Infusorians, and larvae.

Classification.—The classification of the Bryozoans remains as yet in an unsatisfactory condition. D'Orbigny's comprehensive system is largely artificial, and although numerous modifications and improvements have been suggested by later authors, a thorough revision has still to be undertaken.

Lankester divides the class into two very unequal sub-classes as follows: (1) *Holobranchia*, in which the lophophore or row of tentacles is unbroken, and either circular or horse-shoe shaped; and (2) *Pterobranchia*, containing the single genus *Rhabdopleura*, which has the lophophore produced on either side into a plume-like process, so that the tentacles form a discontinuous series.

The *Holobranchia* are again divisible into two unequal groups, named by Nitsche *Ectoprocta* and *Entoprocta*, according as the lophophore surrounds the mouth only, or encloses both the oral and anal orifices. The first of these groups contains the bulk of the known *Bryozoa;* and, furthermore, the marine forms, and all genera capable of preservation in the fossil state, are included in the single order *Gymnolaemata*. This

is distinguished from the remaining order, *Phylactolaemata*, Allman, by the complete abortion of the foot, and by the circular arrangement of the tentacles.

The Mesozoic and recent marine *Gymnolaemata* are almost universally divided into the three sub-orders proposed by Busk, the *Cyclostomata*, *Chilostomata*, and *Ctenostomata*. To these Vine has added a fourth, the *Cryptostomata*, and Ulrich a fifth, the *Trepostomata*; both of which serve mainly for the reception of Palaeozoic forms.

The detailed classification of the Mesozoic and recent *Bryozoa*, especially of the *Chilostomata*, is less settled than that of the ancient types. This non-conformity is due in part to the widely different views prevailing among authors as to the relative value of the various characters upon which the groups are founded; and partly because the mode of growth, and zoarial characters in general, are much less constant, and, therefore, less reliable than is the case among Palaeozoic representatives of the class.

Order 1. GYMNOLAEMATA. Allman.

Sub-Order A. CYCLOSTOMATA. Busk.

(*Bryozoaires centrifugiués*, d'Orbigny, p.p.)

Zoœcia very simple, calcareous, tubular, usually without transverse partitions; the orifices plain, inoperculate, not contracted, occasionally expanded; walls thin, minutely porous; apertural portion of zoœcial tubes more or less raised, bent outwards, free or in bundles; the interspaces with or without solid or tubular strengthening deposits. Marsupia and appendicular organs wanting. Oœcium a large cell set apart for reproductive functions, or a mere inflation of the zoarial surface.

The families and genera of this sub-order are founded almost entirely upon the form of the zoarium, and the arrangement of the zoœcia. The presence or absence of interstitial or accessory cells and vesicular tissue (all strengthening deposits) is also an important character.

Until quite recently it was customary to regard all Palaeozoic Bryozoans as *Cyclostomata*, but the labours of Ulrich and Vine have clearly demonstrated the fallacy of such an assumption. The families *Ceramoporidae* and *Fistuliporidae* are somewhat doubtfully referred to this sub-order, because they agree with its most typical members in having amalgamated and minutely porous walls. Moreover, the latest investigations of Ulrich have shown that the *Ceramoporidae*, which were clearly the progenitors of the *Fistuliporidae*, were in turn derived from an as yet undescribed group of Chazy Bryozoans greatly resembling *Berenicea* and *Apsendesea*.

Family 1. Crisiidae. Busk.

Zoaria dendroid, attached by radical tubes and composed of segments united by corneous joints. Zoœcia tubular, disposed in single or double series. Tertiary and Recent.

Crisia, Lam. Zoaria more or less distinctly articulated, the zoœcia in a single or in two alternating series.

Family 2. Diastoporidae. Busk (emend.)

Zoaria adnate, adhering by the entire base or only at the centre, at other times rising into bifoliate leaves or hollow stems. Zoœcia tubular, the aperture salient, rounded, never clustered. Interstitial cells wanting. Ovicells mere irregular inflations of the surface of the zoarium, with one or more openings. Ordovician to Recent.

Stomatopora, Bronn (*Alecto*, Lam. non Leach), (Figs. 412 and 413). Zoaria delicate, adnate, dichotomously branching. Zoœcia sub-tubular, clavate, or elongate-ovate, arranged in one or more series; apertures sub-terminal, usually smaller than the width of the cell. Ordovician, Jura, Cretaceous, Tertiary, and Recent.

Silurian species like *S. inflata*, Hall, perhaps do not strictly belong to this genus.

D'Orbigny, Haime, and others restriet *Stomatopora* to the uniserial forms, and classify

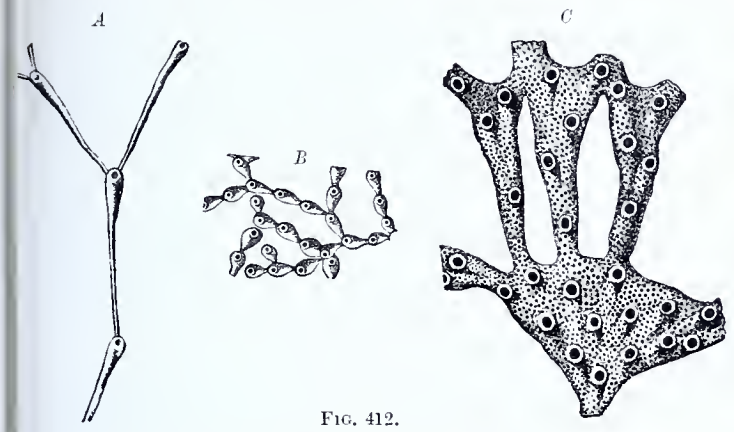


Fig. 412.

A, *Stomatopora tenuissima*, Ulrich. Utica Group; Cincinnati, O. Zoœcia, $^{16}/_{1}$. *B*, *S. inflata*, Hall. Loraine Group; Cincinnati, $^{6}/_{1}$. *C*, *S.* (*Proboscina*) *frondosa*, Nich. Same locality. Portion of large zoarium, $^{12}/_{1}$ (after Ulrich).

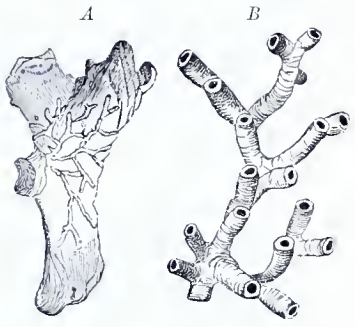


Fig. 413.

Stomatopora dichotoma, Lamx. sp. Great Oolite; Ranville, Calvados. *A*, Zoarium, $^{1}/_{1}$. *B*, same, enlarged.

the multiserial as *Proboscina*, Andouin. Should the latter genus have to be withdrawn, Ulrich would place the multiserial species with *Berenicea*.

Berenicea, Lam. (*Diastopora*, Busk non Lam.), (Fig. 414). Zoaria forming thin, discoid, flabellate, or irregular crusts upon foreign bodies. Zoœcia arranged in irregularly alternating lines. Rare in Ordovician, very abundant in Jura and Cretaceous, less frequent in Tertiary and Recent.

Discosparsa, d'Orb. Differs from *Berenicea* in having obconical or cup-shaped zoaria, attached by centre of the base only. Cretaceous.

Diastopora, Lam. (*Mesenteripora*, Blv.), (Fig. 415). Like *Berenicea*, except that the

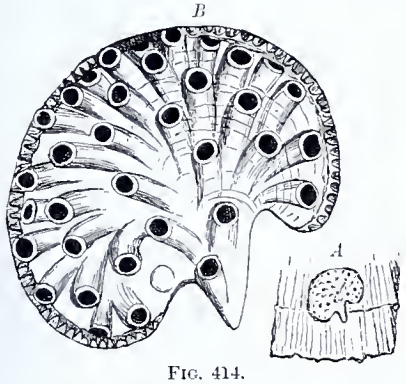


Fig. 414.

Berenicea diluviana, Lamx. Great Oolite; Ranville, Calvados. *A*, Young expansion, $^{1}/_{1}$. *B*, Same, enlarged (after Haime).

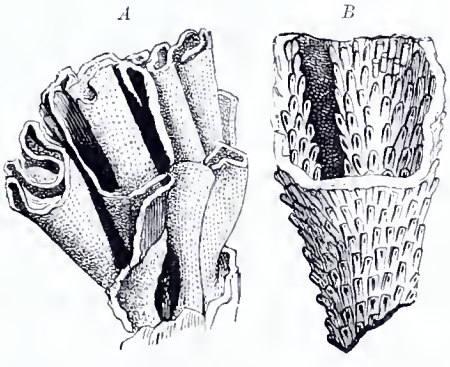


Fig. 415.

Diastopora foliacea, Lamx. sp. Great Oolite; Ranville, Calvados. *A*, Fragment of zoarium, $^{1}/_{1}$. *B*, Enlarged portion of same.

zoarium rises into broad, simple, or convoluted leaves, composed of two layers of zoœcia grown back to back. Very abundant in the Jura, less common in Cretaceous and Tertiary.

Bidiastopora, d'Orb. Like *Diastopora*, but the zoaria forming only narrow, parallel-edged branches. Cretaceous.

Diastoporina, Ulrich, Ordovician; *Hederella* and *Hernodia*, Hall, Devonian; and *Reptaria*, Rolle, Devonian.

Family 3. **Idmoneidae.** Busk.

Zoaria forming free or adnate, variously compressed branches. Zoœcial apertures rounded, more or less elevated, usually arranged in transverse rows on two faces of the branches; sometimes the two faces are confluent. Dorsal surface of the branches without zoœcia, but often occupied by numerous small tubular pores, which may also occur near the apertures. Sac-like ovicells with but a single opening. Ordovician to Recent.

Idmonea, Lam. (*Reptotubigera*, *Crisina*, d'Orb.), (Fig. 416). Repent or erect, simple or branching. Branches usually triangular, two of the faces carrying the zoœcial apertures, which are generally arranged in alternating transverse series. Jura to Recent.

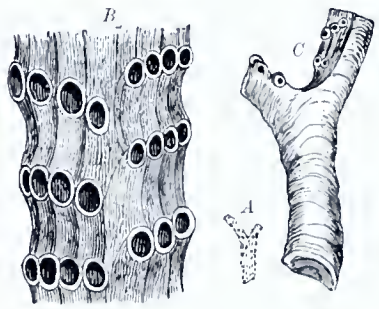


Fig. 416.

Idmonea dorsata, Hagw. Upper Cretaceous; Maestricht. *A*, Branch, 1/1. *B*, Upper, and *C*, Lower side, highly magnified.

Fig. 417.

Protocrisina exigua, Ulrich. Trenton Group; Trenton, N.Y. Branches of a large expansion, 12/1.

Bisidmonea, d'Orb. Quadrate, simple, or branching stems, bearing zoœcial apertures on all faces. Cretaceous.

Filisparsa, d'Orb. Branches compressed dorso-frontally; apertures irregularly disposed; otherwise like *Idmonea*. Cretaceous.

Filicavea and *Filicrisina*, d'Orb. Cretaceous.

Hornera, Lam. Zoaria with free or anastomosing, generally sub-cylindrical branches. Zoœcial apertures more or less irregularly distributed. Cretaceous to Recent.

Reticulipora and *Retecava*, d'Orb. Zoaria reticulated; branches greatly compressed laterally. Cretaceous.

Bicrisina and *Sulcocava*, d'Orb. (*Laterocava*, d'Orb.) Cretaceous.

Protocrisina, Ulrich (Fig. 417). Narrow, bifurcating branches, celluliferous on one side only. Zoœcia sub-tubular, with prominent circular apertures arranged in intersecting diagonal series. Small pores, apparently communicating with interior of the zoœcia, irregularly distributed over both faces of the branches. Ordovician.

Family 4. **Entalophoridae.** Reuss.

Zoaria ramose; branches free, sub-cylindrical, with rounded and more or less prominently exserted zoœcial apertures opening on all sides. (?) Without accessory or interstitial pores of any kind. Ordovician to Recent.

Entalophora, Lam. (*Pustulopora*, Blv.), (Fig. 418). Zoœcial tubes disposed about an imaginary axis, and with rounded, more or less prominent apertures. Jura to Recent.

Spiropora, Lam. (*Laterotubigera*, d'Orb.), (Fig. 419). Like the preceding, but apertures arranged in regular, spiral, or transverse linear series, and closely situated. Zoœcial tubes disposed about a definite central axis or axial tube. Jura to Recent.

Mitroclema, Ulrich, Ordovician; *Clonopora*, Hall, Devonian; *Peripora*, d'Orb., Cretaceous.

Diploclema, Ulrich. Similar to *Entalophora*, but with branches spreading in the

Fig. 418.

Entalophora virgula, Hagw. Planer; Plauen, Saxony.

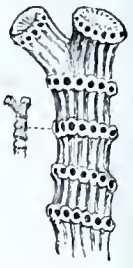


Fig. 419.

Spiropora verticillata, Goldf. Upper Cretaceous; Maestricht (after Hagenow).

same plane, slightly compressed, and divided into two equal parts by a wavy mesial lamina. Silurian.

? *Clausa*, d'Orb. (*Claviclausa*, (?) *Sparsieavea*, d'Orb.) Like *Entalophora*, but having the zoœcial apertures surrounded by shallow interstitial cells, the mouths of which are covered in the perfect condition. Cretaceous.

? *Petalophora*, Lonsd. (*Cavea*, d'Orb. ; *Canalipora*, Hagw.) Cretaceous.

Family 5. **Fasciporidae.** d'Orbigny (emend.)

Zoœcia tubular, opening in clusters at the growing extremities, and in linear or quincuncial series on the sides of the lamelliform, or obconical zoaria. Accessory pores wanting. Cretaceous.

Fascipora, d'Orb. (*Faseiporina*, d'Orb.) Zoaria compressed, sub-ramose to lamelliform. Apertures arranged quincuncially or somewhat irregularly on both sides, and on the more or less expanded growing extremities of the branches and lamellae. The lamelliform species resemble *Diastopora*, but are without a mesial lamina.

Semifaseipora, d'Orb. (Fig. 420). Zoaria cup- or funnel-shaped, with only the outer surface poriferous, the inner covered by an epitheca. Poriferous face thrown into vertical ridges bearing the salient tubular mouths of one or more rows of zoœcia. At the upper edge the ridges pass into large clusters of apertures.

Conotubigera and *Serietubigera*, d'Orb. Closely related to the preceding.

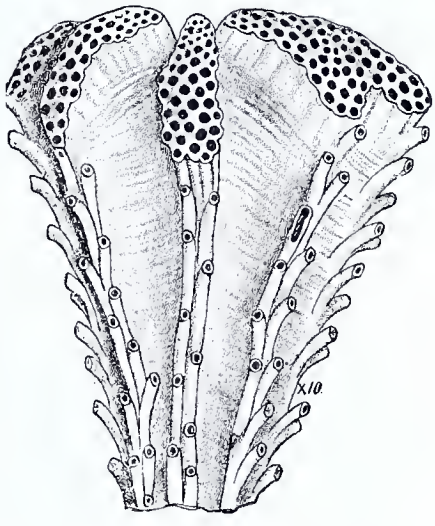


Fig. 420.

Semifascipora variabilis, d'Orb. Cretaceous ; France. Side view of zoarium, $^{10}/_{1}$.

Family 6. **Fascigeridae.** d'Orbigny (emend.)

Zoaria repent or erect, lamelliform or branching, generally the latter. Zoœcial apertures arranged in bundles or clusters, in which they are contiguous. Jura to Recent.

Fig. 421.

Filifascigera, megaera, Lonsd. Upper Cretaceous; Vincentown, N.J. Specimen seen from above and from the side, $^{12}/_{1}$ (after Ulrich).

Filifascigera, d'Orb. (Fig. 421). Zoaria repent, irregularly branching. Apertures erect, in successive groups of from two to five or more. Growth terminal. Cretaceous and Tertiary.

Reptofascigera, d'Orb. (*Semitubigera*, d'Orb.) Zoaria repent, growth terminal. Apertures in two series of clusters directed alternately to the right and left. Cretaceous.

Theonoa, Lam. (*Tilesia*, Lam. ; *Faseicularia*, M. Edw. ; *Lopholepis*, Hagw. ; *Multifaseigera*, etc., d'Orb.), (Fig. 422). Zoaria lamelliform or massive, usually free, with an epitheca on lower face ; sometimes in superposed layers. Apertures in elevated clusters, somewhat irregularly distributed, more or less elongated. Growth peripheral. Jura to Tertiary.

Fasciculipora, d'Orb. (*Fungella*, Hagw.), (Fig. 423). Zoaria erect, simple, or branching. Apertures crowded, limited to the convex and usually expanded upper extremities of the branches. Sides of stems usually without pores. Jura to Tertiary.

Frondipora, Imperato. Zoaria bushy, attached at the base ; branches free or

anastomosing. Zoœcial apertures on one side only; branches otherwise without pores. Cretaceous to Recent.

Unicytis, d'Orb. Like the preceding, except that the non-elevated portions of the surface of the branches are occupied by interstitial cells. Cretaceous.

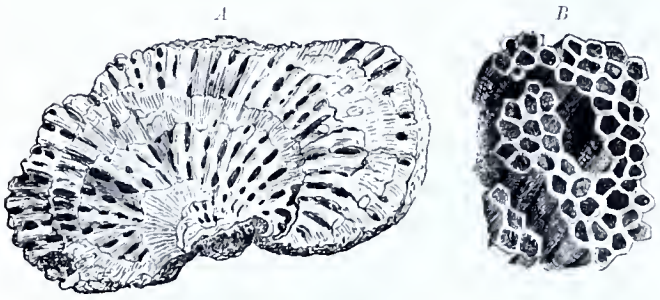


Fig. 422.

Theonoa aurantium, M. Edw. Crag; Sussex. *A*, Zoarium broken open in a vertical plane, 1/1. *B*, Enlarged portion of upper surface.

Fig. 423.

Fasciculipora incrassata, d'Orb. Upper Cretaceous; Meudon, near Paris. Terminal fragment, nat. size and enlarged (after d'Orbigny).

Osculipora, d'Orb. (Fig. 424). Differs from *Frondipora* in having the apertures in two alternating rows of more or less strongly projecting clusters. Cretaceous.

Fig. 424.

Osculipora truncata, Hagw. Upper Cretaceous; Maestricht, Holland. Fragment, 1/1 and enlarged (after Ulrich).

Fig. 425.

Truncatula repens, Hagw. Upper Cretaceous; Maestricht. Lower and upper sides of zoarium, enlarged (after Hagenow).

Truncatula, Hagw. (Fig. 425). Distinguished from *Osculipora* by having one face only covered with epitheca, the other (convex side) exhibiting numerous longitudinally arranged interstitial cells. Cretaceous.

Desmeopora, Lonsd. (*Semicytis*, d'Orb.); *Discofascigera*, d'Orb. Cretaceous.

Cyrtopora, Hagw. Sub-cylindrical stems with prominent clusters of four or more zoœcial apertures scattered over the entire surface. Interspaces smooth. Cretaceous to Recent.

Plethopora, Hagw. Clusters larger than in the preceding, and the depressed interspaces occupied by small cells. Cretaceous.

Family 7. Lichenoporidae.

Zoaria simple or composite, discoid or massive, adhering by more or less of the under surface. Zoœcial apertures on the upper surface, arranged in radial series. Jura to Recent.

Discocytis, d'Orb. (*Pelagia*, Mich. non Lam.; *Bicavea*, *Radiocavea*, d'Orb.), (Figs. 426, 427). Zoaria cup-shaped, obconical, or discoid, often pedunculate, poriferous on the under and outer sides. The concave upper side with a decidedly radial structure; zoœcial apertures scarcely distinguishable from pores on the sides of the zoarium. Cretaceous.

Apsendesia, Lam. (*Pelagia*, Lam.; *Defrancea*, Bronn; *Radiofascigera*, etc., d'Orb.; ? *Buskia*, Reuss), (Figs. 428, 429). Zoaria simple or composite, discoid or lamelliform, attached by a peduncle or by the whole under surface. Interstitial cells wanting. Jura to Recent.

Lichenopora, Defr. (*Discocavea*, *Radiocavea*, etc., d'Orb.; *Stellipora*, Hagw. non Hall;

Discoporella, Gray), (Figs. 430, 431). Like *Apsendesia*, except that interstitial cells occur

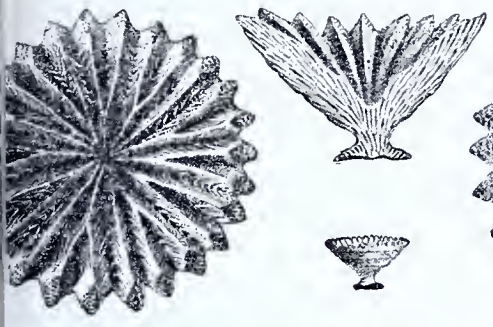


Fig. 426.

Discocytis endesii, d'Orb. Upper Cretaceous; France. Specimen 3/4 natural size, and three views of same enlarged (after d'Orbigny).

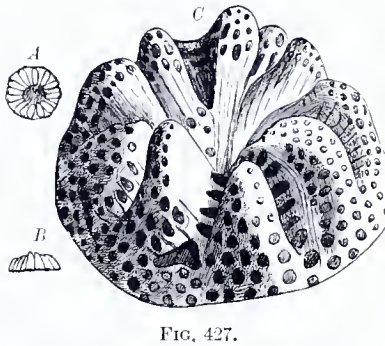


Fig. 427.

Discocytis diadema, Goldf. sp. Upper Cretaceous; Maestricht. *A*, Zoarium, 1/1. *B*, Profile of same. *C*, Upper surface, enlarged.

between the elevated rows of zoœcial apertures, on a depressed space at the centre of each disk, and often also on the under surface of the zoarium. Jura to Recent.

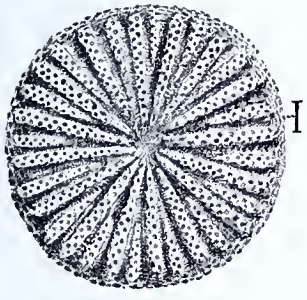


Fig. 428.

Apsendesia Gaudryana, d'Orb. Upper Cretaceous; France. Upper surface, 8/1.

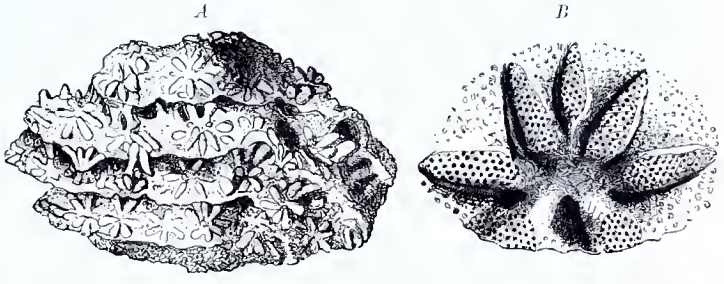


Fig. 429.

Apsendesia (*Buskia*) *tubulifera*, Roemer sp. Astrupp, Westphalia. *A*, Zoarium, 1/1. *B*, Cluster of zoœcial apertures, enlarged.

Stellocavea, d'Orb. Zoaria discoidal, the upper surface exhibiting the salient edges of

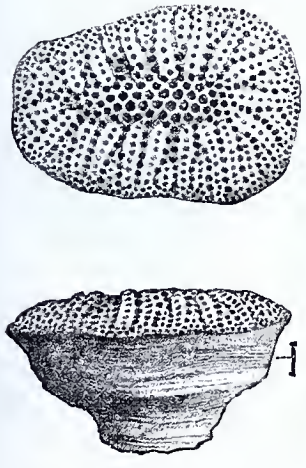
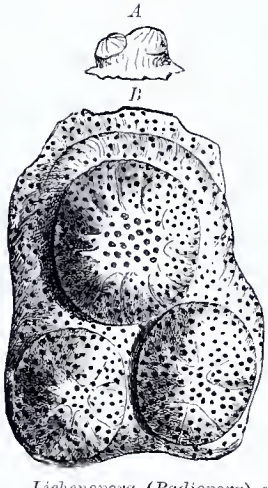


Fig. 430.

Lichenopora pocillum, d'Orb. Cretaceous; France (after d'Orbigny).



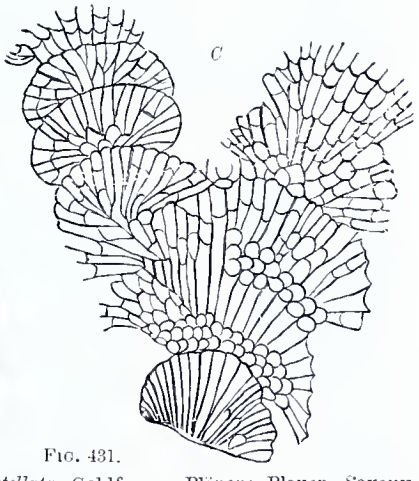


Fig. 431.

Lichenopora (*Radiopora*) *stellata*, Goldf. sp. Pläner; Plauen, Saxony *A*, Zoarium, 1/1. *B*, Same, enlarged. *C*, Vertical section of specimen from Greensand of Essen.

numerous radially arranged plates, few of them reaching the centre. Zoœcial tubes

opening on the two opposite sides of plates. Depressed interspaces occupied by interstitial cells. Cretaceous.

? *Multicavea*, d'Orb. Zoaria ramose, the stems poriferous on all sides, interstitial cells composing the greater part. Apertures forming short stellate series disposed at close intervals over the surface of the branches. Cretaceous.

Family 8. **Cerioporidae.** Busk.

Zoaria multiform, encrusting, lamellar, bulbous, lobate, digitate, or ramose, composed of closely arranged thin-walled tubes. The latter sometimes completely separated by angular interstitial cells. Walls of neighbouring tubes thoroughly amalgamated and pierced by numerous pores. Trias to Recent.

The *Cerioporidae* greatly resemble many of the Palaeozoic *Trepostomata*, but, as a rule, may be readily distinguished by the complete amalgamation and porous nature of their zoœcial walls.

Ceriopora, Goldf. (*Ceriocava*, d'Orb.), (Fig. 432). Zoaria encrusting, massive, lobate, or ramose, often consisting of two or more superposed layers of tubes. The latter are sub-equal, in close contact, of one kind only, and their round or polygonal apertures cover the entire upper surface of the colony. Very abundant in the Alpine Trias, sparse in the Jura, but frequent again in the Cretaceous.

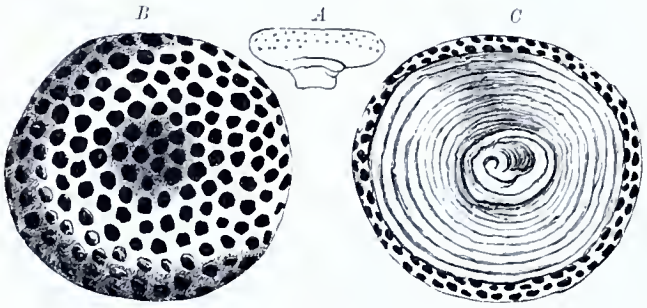


Fig. 432.

Ceriopora spongites, Goldf. Greensand; Essen. *A*, Zoarium, 1/1. *B*, *C*, Upper and lower sides, enlarged.

Heteropora, Blainv. (*Multicresis*, *Nodicresis*, *Zonopora*, *Polytremata*, etc., d'Orb), (Fig. 433). Zoarium variable, generally ramose, sometimes composed of several layers of tubes. Apertures rounded, the peristome often slightly raised. Interstitial tubes numerous, angular, usually surrounding the zoœcia completely, their orifices closed when perfect.

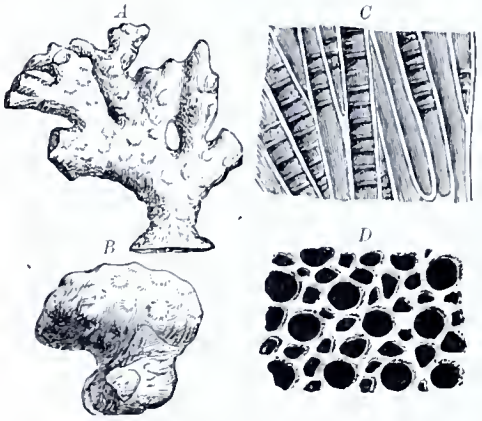


Fig. 433.

Heteropora pustulosa, Mich. Great Oolite; Ranville, Calvados (after Hanne). *A*, *B*, Zoarium, 1/1. *C*, Vertical section. *D*, Upper surface, enlarged.

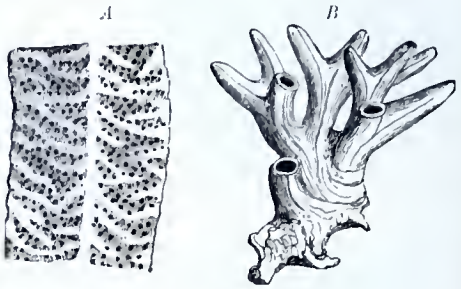


Fig. 434.

Neuropora angulosa, Goldf. sp. Upper Jura; Oerlingen, near Ulm. *A*, Natural size. *B*, Portion of surface, enlarged.

They are frequently gathered into clusters and separate the true zoœcia into zones or patches. Very abundant in Jura and Cretaceous, rare in Tertiary and Recent.

Hetcroporella, Busk. Like the preceding, but growth-habit encrusting. Cretaceous and Tertiary.

? Ditaxia, Hagw. Zoaria ramose, branches flattened, consisting of two layers of tubes grown together back to back. Otherwise like *Heteropora*. Cretaceous.

Chilopora, Haime. Zoaria erect, lamelliform; apertures rather large, rounded or sub-triangular, oblique, with the lower half of the margin elevated. Interstitial cells numerous, much smaller than the zoœcia. Jura.

Neuropora, Bronn (*Chrysaora*, Lam.; *Filicava*, d'Orb.), (Fig. 434). Zoaria generally irregularly ramose, attached at the base, composed of sub-equal tubular zoœcia. These open on all exposed parts of the surface, save on certain variously arranged, more or less raised, thin solid ridges. Jura and Cretaceous.

Acanthopora, d'Orb. Zoaria ramose, consisting of but one kind of zoœcial tubes. Surface studded with numerous solid conical or spine-like prominences. Jura and Cretaceous.

Families doubtfully referable to the Cyclostomata.

Family 9. **Ceramoporidae.** Ulrich.

Zoaria usually encrusting, sometimes discoid, lamellate, massive, or forming more or less regular hollow branches; rarely bilobiate. Clusters of mesopores and of zoœcia, larger than the average, occur at regular intervals. Zoœcial apertures usually oblique, of sub-triangular, ovate, or polygonal form; lunarium present, appearing at the surface as a prominent overarching hood, or as a slightly elevated portion of the margin, of crescentic form, with the ends projecting more or less into the aperture. Mesopores or interstitial cells generally present, always irregular, and usually without diaphragms. A few horizontal diaphragms often present in the zoœcial tubes. Walls minutely porous, composed of intimately connected and irregularly laminated tissue. Ordovician and Silurian.

This is one of the largest and most important of the families of Palaeozoic Bryozoans, and is especially common in the Trenton and Cincinnati Groups. The earliest forms resemble *Berenicea* and *Apsendesia*; while *Ceramoporella*, *Chiloporella*, and especially *Bythotrypa*, may be regarded with reasonable confidence as the progenitors of the *Fistuliporidae*. At any rate the connection between the two families is so intimate as to forbid any wide separation.

Ceramopora, Hall. Discoidal, free, or attached by the centre of the base. Under surface with one or more layers of small irregular cells. Zoœcia opening on the upper surface, large, oblique, imbricating, and radially arranged about the depressed centre. Mesopores irregular, short, numerous at the centre of the colony, decreasing toward the periphery. Silurian.

Fig. 435.

Ceramoporella distincta, Ulrich. Lower Trenton, Minnesota. Surface of parasitic expansion, $^{12}/_{1}$ (after Ulrich).

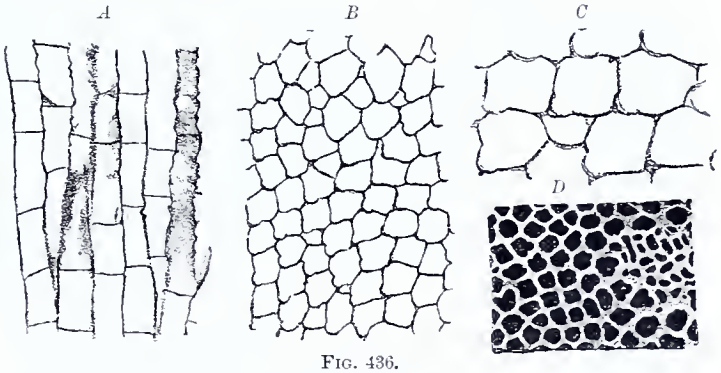


Fig. 436.

Crepipora perampla, Ulrich. Trenton; Minnesota. *A*, Vertical section. *B*, Transverse section, $^{7}/_{1}$. *C*, Same, $^{14}/_{1}$, showing lunaria. *D*, Surface of *C. simulans*, Ulrich, $^{9}/_{1}$ (after Ulrich).

Ceramoporella, Ulrich (Fig. 435). Zoaria encrusting, becoming massive by superimposition of numerous thin layers. Zoœcial tubes short, walls thin, apertures more

or less oblique, hooded, commonly of oval shape. Mesopores abundant, often completely isolating the zoœcia. Apertures closed by a thin calcareous sheet at maturity. Abundant in Ordovician. *C. distincta*, Ulrich.

Crepipora, Ulrich (Fig. 436). Encrusting, lamellate, or massive, in one case forming hollow branches. Zoœcial tubes long, partitioned off by a moderate number of diaphragms. Mesopores almost entirely restricted to the maculae, which are distributed over the surface as minutely porous elevations or depressions. Apertures very slightly oblique, angular, or sub-pyriform. Lunarium well-defined in perfect specimens, best shown in tangential sections. Ordovician, ? Silurian.

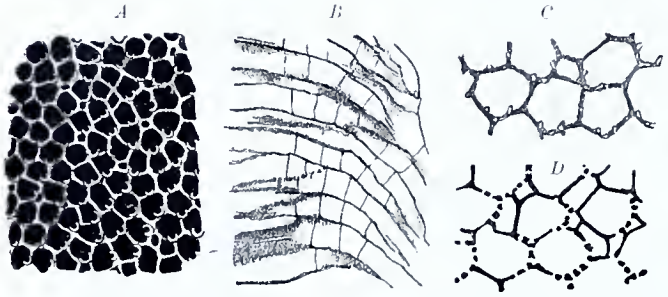


Fig. 437.

Anolotichia impolita, Ulr. Lower Trenton; Minnesota. *A*, Surface, $^{6}/_{1}$. *B*, Vertical section, $^{6}/_{1}$. *C*, Tangential section, $^{12}/_{1}$, showing tubes of lunarium. *D*, Tangential section of *A. ponderosa*, Ulr., from the Cincinnati formation at Wilmington, Ill., showing numerous lunarial tubes (after Ulrich).

Fig. 438.

Ceramophylla frondosa, Ulr. Black River Shales; Minnesota. *A*, Zoarium, $^{2}/_{3}$. *B*, Surface of same, $^{6}/_{1}$. *C*, Two zoœcia of a tangential section, $^{12}/_{1}$. *D*, Right half of a vertical section, $^{12}/_{1}$ (after Ulrich).

Anolotichia, Ulrich (Fig. 437). Zoaria large, ramose, or digitate, consisting of long, sub-polygonal tubes intersected by remote diaphragms. Mesopores never very numerous. Lunarium slightly elevated at the surface, traversed internally by two to six minute, vertical, closely tabulated tubes. Ordovician.

Diamesopora, Hall (*Coeloclema*, Ulrich). Hollow branches, lined internally with a striated epitheca. Zoœcia as in *Ceramoporella*, but with thicker walls. Ordovician and Silurian.

Fig. 439.

Diamesopora trentonensis, Ulr. Trenton; Minnesota. Two fragments, $^{2}/_{3}$, and one $^{6}/_{1}$.

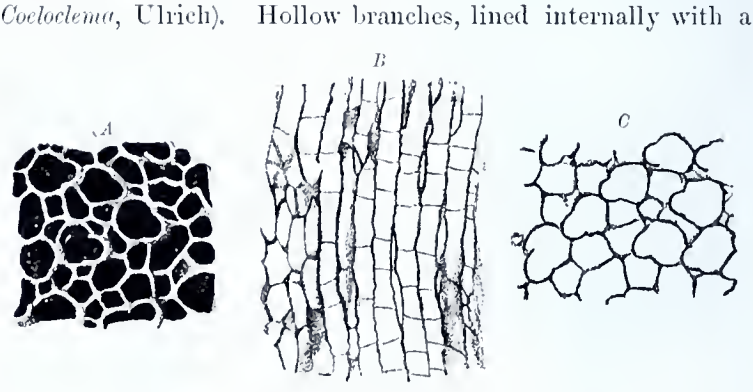


Fig. 440.

Bythotrypa laxata, Ulr. Trenton; Minnesota. *A*, Surface, $^{14}/_{1}$. *B*, Vertical section, $^{7}/_{1}$. *C*, Transverse section, $^{14}/_{1}$ (after Ulrich).

Ceramophylla and *Chiloporella*, Ulrich. Ordovician.

Bythotrypa, Ulrich (Fig. 440). Zoaria massive or lamellate. Zoœcial tubes long, intersected by thin diaphragms. Lunarium large; mesopores numerous, open at the surface, forming interiorly a very loose vesicular tissue. Ordovician.

Scenellopora, Ulrich. Zoaria simple, pedunculate; under surface with an epitheca,

the upper slightly concave and celluliferous. Zoœcia with slightly oblique, sub-circular apertures, radially arranged on the summits of low ridges. Very suggestive of *Apsendesia*. Certain Chazy species are composite, and allied to *Ceramoporella*. Ordovician.

Spatiopora, Ulrich (Fig. 441). Zoaria forming thin crusts, especially on *Orthoceras*. Apertures irregular; lunarium scarcely perceptible. Mesopores, when present, chiefly in maculae. Interspaces often with large blunt spines (? acanthopores). Ordovician.

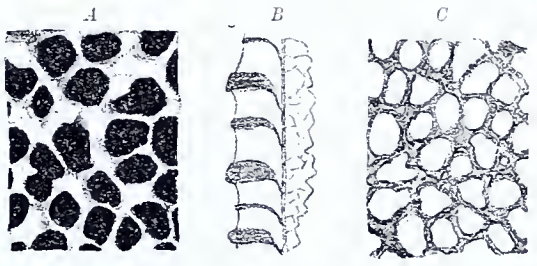


FIG. 441.

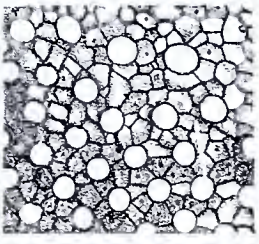
Spatiopora aspera, Ulr. Cincinnati Group; Hamilton, O. *A*, Surface. *B*, Vertical section. *C*, Tangential section; all 14/1 (after Ulrich).

Family 10. **Fistuliporidae.** Ulrich.

Zoaria massive, laminar, or ramose, the surface exhibiting at regular intervals "maculae" or "monticules" composed of clusters of vesicles and of zoœcia slightly larger than the average. Lunarium more or less developed. Zoœcial tubes never angular, thin-walled, and with horizontal diaphragms; apertures closed by perforated operculum. Interspaces occupied by vesicular tissue. Cell walls minutely porous. Silurian to Permian; climax in Devonian.

Waagen and Wentzel have recently referred this family to the Corals (cf. *ante*, p. 105), but their reasons for doing so rest obviously upon insufficient observation. Not only are the members of this family derived from the *Ceramoporidae*, as noted above, which are undoubted Bryozoans, but some of them possess ovicells, thus abundantly proving their Bryozoan nature.

Fistulipora, M'Coy (*Lichenalia*, *Thallostigma*, Hall; *Didymopora*, Ulrich; *Dybowskiella*, Waag. and W.), (Fig. 442). Zoaria massive, lamellate, more rarely ramose, parasitic, or free; under surface with wrinkled epitheca. Zoœcia sub-radially arranged about the surface maculae; apertures ovoid, sub-triangular, or pyriform, according to the degree in which the lunarium is developed; interiorly with thin walls, and a small number of complete horizontal diaphragms. Interspaces smooth or granular, occupied internally by one or more series of vesicles. Common from Silurian to Sub-Carboniferous; less frequent in Coal Measures and Permian.



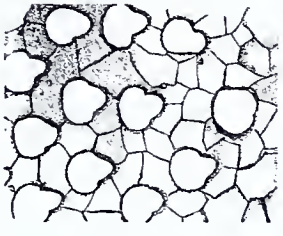


FIG. 442.

Fistulipora astrica, Ulr. Hamilton; New Buffalo, Iowa. Tangential section, 14/1.

Cyclotrypa, Ulrich (n. gen. or sub-gen.), (Fig. 443). Like *Fistulipora*, but the lunarium obsolete, and zoœcial tubes circular in transverse section. Devonian. *Fist. communis* and *F. collina*, Ulrich.

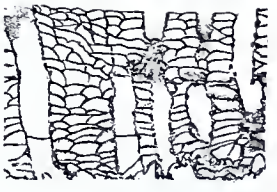


FIG. 443.

Cyclotrypa communis, Ulr. Hamilton; New Buffalo, Iowa. Vertical and tangential sections, 14/1 (after Ulrich).

Eridopora, Ulrich (*Pileotrypa*, Hall). Zoaria thin, parasitic. Zoœcia with oblique, sub-triangular, or ovoid apertures. Lunarium very prominent. Niagara to Coal Measures.

Chilotrypa, Ulrich (*Coelocaulis*, Hall). Zoaria small, ramose, with a narrow, irregularly contracting and expanding axial tube. Apertures elliptical, oblique, the lower margin thick and elevated, the wall thin above. Diaphragms few or absent.

Interstitial vesicles filled by a dense calcareous deposit near the surface. Silurian and Sub-Carboniferous.

Meekopora, Ulrich (Fig. 444). Zoaria bifoliate, sometimes branching, the median laminae thin, flexuous. Oblique apertures all directed toward the distal margin of the zoarium or branch. Lunarium moderate or obsolete; diaphragms numerous and often recurved. Ovicell rather large, showing at the surface as a convex space with a small apical opening. Sub-Carboniferous.

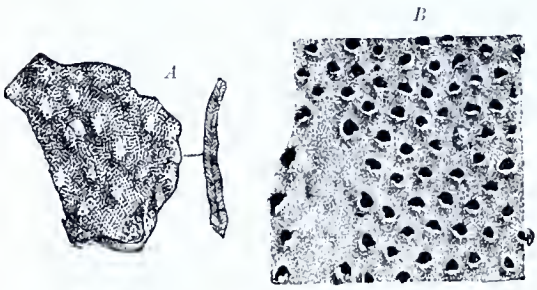


Fig. 444.

Meekopora eximia, Ulr. Chester Group; Monroe Co., Ill. *A*, Specimen from the side and edge, 3/4. *B*, Surface of same, 7/1. *C*, Portion showing ovicell, 14/1 (after Ulrich).

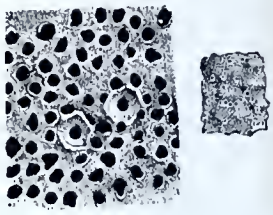


Fig. 445.

Strotopora forcolata, Ulr. Keokuk Group; Bentonsport, Iowa. Part of expansion, 3/4, and surface of same, 7/1, showing zoœcial apertures and broken ovicells (after Ulrich).

Strotopora, Ulrich (Fig. 445). Zoaria ramose, with irregular branches. Large, abruptly spreading cells (regarded as broken ovicells), distributed among the zoœcia on ordinary specimens; when perfectly preserved they appear as strongly convex elevations with a small opening on one side. Devonian and Sub-Carboniferous.

Lichenotrypa, Ulrich. First stages like *Fistulipora*, after which large spines and irregular thin walls are thrown up about the apertures. Devonian.

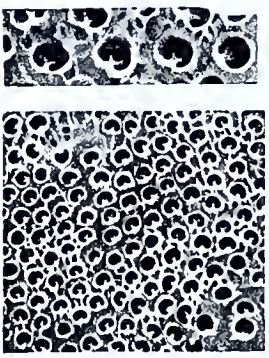


Fig. 446.

Buskopora dentata, Ulr. Hamilton; Falls of the Ohio. Portions of surface, 7/1 and 14/1 (after Ulrich).

Buskopora, Ulrich (*Odontotrypa*, *Glossotrypa*, Hall), (Fig. 446). Like *Fistulipora*, but lunarium remarkably developed, projecting as a strong, bidenticulate process nearly half across the aperture. Devonian.

Selenopora, Hall (*Favicella*, Hall). Zoaria laminar, encrusting. Interzoœcial spaces occupied by two series of small vesicles, separated by strongly elevated walls. These bound the hexagonal spaces in which the zoœcial apertures are situated. Lunarium obsolete. Devonian.

Pinacotrypa, Ulrich; (?) *Botryllopora*, Nicholson. Devonian.

Family 11. **Ceidae**. d'Orbigny.

Zoaria ramose, bifoliate, or uni-lamellate. Zoœcia tubular, sub-equal, their walls thin at first, but thickening gradually toward the periphery, where the cavity suddenly dilates in such manner that the rounded or elliptical aperture lies at the bottom of an hexagonal depression. Interstitial cells wanting. Cretaceous.

The systematic position of this family is highly problematical. It appears to have certain affinities with the *Trepostomata*, but its removal to that vicinity is hardly feasible until a thorough comparison of Palaeozoic and Mesozoic Bryozoans shall have been made.

Semicea, d'Orb. (*Reptocea*, d'Orb., p.p.); *Diseocea*, Pergens.

Cea, d'Orb. Zoaria forming flattened branches or broad lamellae, celliferous on both sides.

Filicea, d'Orb. (*Laterocea*, d'Orb.), (Fig. 447). Zoaria erect, with sub-cylindrical branches bearing apertures on all sides.

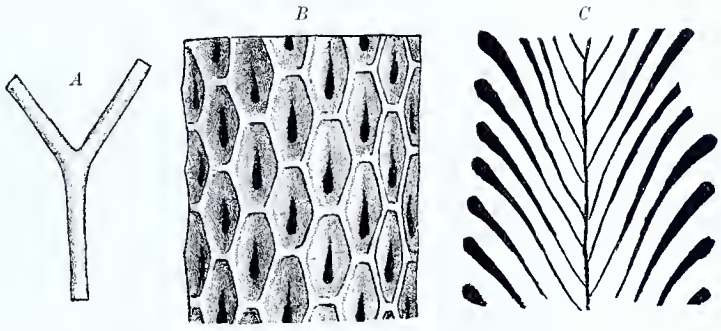


Fig. 447.

Filicea velata, Hagw. sp. Upper Cretaceous; Maestricht, Holland. *A*, Branch, 1/1. *B*, Surface of same enlarged. *C*, Vertical section (after d'Orbigny).

Family 12. Meliceritidae.

Zoaria ramose, bifoliate, or uni-lamellate. Zoœcial tubes dilating outwardly, with perforated walls. Front of zoœcia partly covered by a perforated plate. Vicarious avicularia scattered among the zoœcia. Cretaceous.

The members of this family differ widely from the true *Cyclostomata*. They may be Mesozoic representatives of the Palaeozoic *Cryptostomata*, some of which, particularly *Proutella*, they greatly resemble. But, on the other hand, the presence of avicularia, which are as yet entirely unknown among Palaeozoic Bryozoans, perhaps indicates even stronger affinities with the *Chilostomata*.

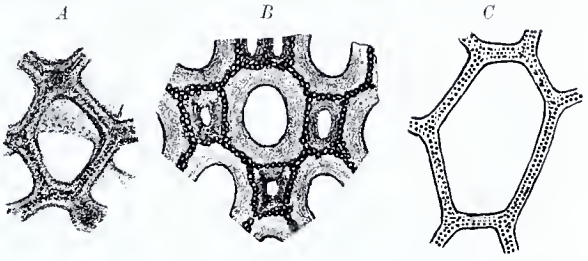


Fig. 448.

Structure of walls and parenchymal cord in *Homotrypa callosa*, Ulr. (*A*, 35/1); *Stictoporella frondifera*, Ulr. (*B*, 35/1); and *Retepora columnifera*, Busk. Recent. (*C*, 60/1.)

Semielea, d'Orb. (*Reptelea*, etc., d'Orb.); *Retelea*, *Clausimultelea*, d'Orb.

Elea, d'Orb. Flattened, branching, or anastomosing stems, or broad leaves, poriferous on both sides.

Meliceritites, Roemer (*Escharites*, Roem.; *Inversaria*, Hagw.; *Nodelea*, *Multelea*, d'Orb.) Cylindrical branching stems, poriferous on all sides.

Sub-Order B. TREPOSTOMATA. Ulrich.[1]

Zoœcia directly superimposed upon one another so as to form long tubes intersected by straight or curved partitions (diaphragms and cystiphragms), representing the covers and

[1] [Two regions of the zoœcial tubes are distinguishable, an axial or "immature" region, in which the diaphragms are remote, the walls thin, and the tubes prismatic through contact; and a peripheral or "mature" region, in which the tubes bend outward, the walls are thickened and otherwise modified, the transverse partitions more abundant, and interzoœcial elements (acanthopores, mesopores, or mere strengthening tissue) are developed.

Waagen and Wentzel and others erroneously assert that the mesopores and acanthopores, occurring so commonly in this sub-order, are young zoœcia or "corallites." With very few exceptions, these really very different elements are not developed until the zoarium has reached the mature stage, in which new zoœcia cease to be given off. The origin of mesopores (*i.e.* all cells occupying interzoœcial spaces, whether invested with separate walls or not) is due to the same necessity which

floors of successive layers. Zoœcial covers with a small, usually sub-central orifice. Monticules or maculae (containing cells differing from the average in size, or in having their apertures elevated) regularly distributed over the surface.

Family 1. **Monticuliporidae.** Nicholson (emend. Ulrich).

Zoaria massive, discoid or lamellar, ramose or bifoliate. Zoœcial apertures polygonal, rounded, or irregularly petaloid. Mesopores occasionally wanting, in other cases numerous, angular, and crossed by crowded diaphragms. Acanthopores abundant, usually small. Cystiphragms always present in the mature region. Ordovician to (?) Devonian.

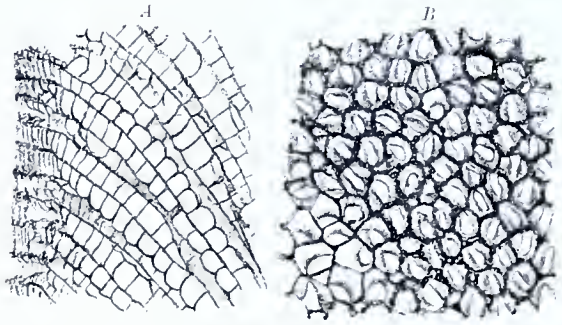


Fig. 449.

Monticulipora arborea, Ulr. Trenton; Minnesota. Vertical (*A*) and tangential (*B*) sections, $^{14}/_{1}$ (after Ulrich).

The incomplete, curved, transverse partitions, termed cystiphragms by Ulrich, are the principal peculiarity of this family. It is possible that they represent oviecils, but their significance can only be conjectured.

Monticulipora, d'Orb. (Fig. 449). Zoaria massive, lobate, or lamellate, encrusting or free. Surface with monticules or plain. Zoœcia polygonal, mostly thin-walled. Mesopores very few or absent. Acanthopores more or less numerous, small. Ordovician, (?) Devonian.

Atactoporella, Ulrich (Fig. 450). Zoaria generally encrusting, rarely lobate or sub-ramose. Zoœcia with very thin inflated walls, the apertures irregularly petaloid.

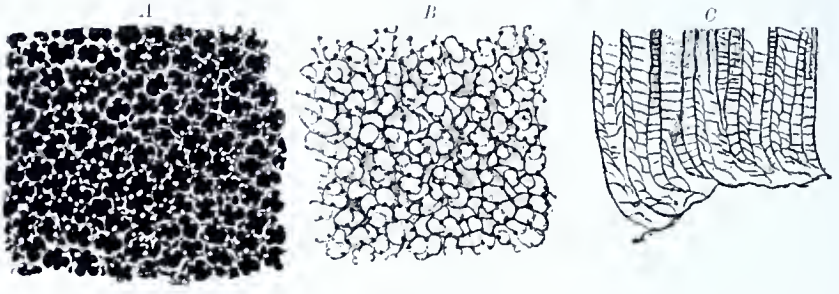


Fig. 450.

Atactoporella typicalis, Ulr. Black River Group; Minnesota. Surface (*A*), tangential (*B*), and vertical (*C*) sections, $^{14}/_{1}$ (after Ulrich).

Mesopores numerous, frequently isolating the zoœcia, largely filled by a secondary deposit. Ordovician.

Peronopora, Nich. (emend. Ulrich). Similar to the preceding, but zoaria bifoliate, and zoœcial walls thicker, not inflected by the acanthopores, and more ring-like in transverse section. Ordovician.

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leads to the distal thickening of the zoœcial tubes, namely, that of filling up spaces occasioned by the growth of tubes at the periphery, and by the change in direction of the tubes.

Some of the tubes provisionally included under the term mesopores, like some of the acanthopores, were doubtless occupied by specially modified polypides, which probably find their homologues in the avicularia and vibracula of recent *Chilostomata*. But many of the mesopores which are not invested by separate walls are to be regarded as mere interspaces between the zoœcial tubes, and the purpose of their transverse partitions is to support the walls of the latter, as well as to assist intercommunication by means of the zoarial parenchymal cord.]

Homotrypa, Ulrich (Fig. 451). Generally ramose, sometimes frondescent. Zoœcial tubes with very thin and finely crenulated walls, and remote diaphragms in the

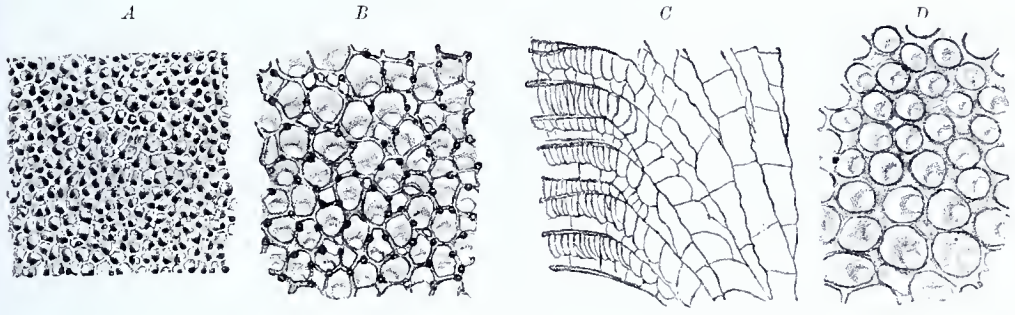

Fig. 451.

Homotrypa subramosa, Ulr. Trenton; Minnesota. *A*, Surface. *B*, *D*, Tangential sections. *C*, Vertical section, $^{14}/_{1}$.

axial region. Cystiphragms, isolated or in series, developed in peripheral region only. Apertures polygonal or sub-circular. Mesopores usually few and in clusters. Acanthopores generally present. Ordovician.

Prasopora, Nich. and Eth. (Fig. 452). Zoarium usually free in adult stage, with wrinkled epitheca on lower surface. Zoœcial tubes prismatic or cylindrical, thin-

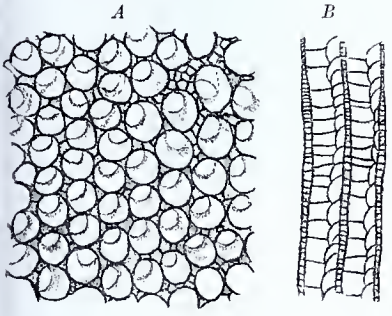

Fig. 452.

Prasopora simulatrix, Ulr. Trenton; Kentucky. *A*, Transverse, and *B*, Vertical section, $^{14}/_{1}$ (after Ulrich).

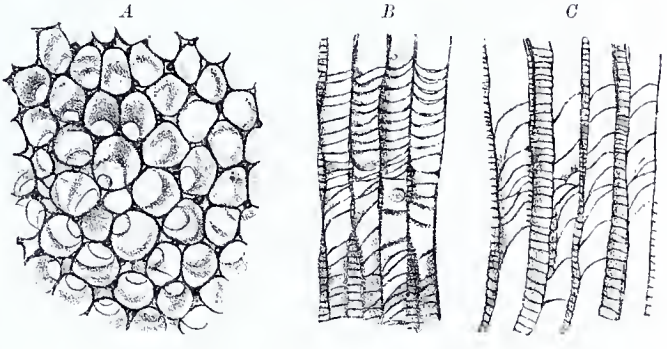

Fig. 453.

Mesotrypa infida, Ulr. Black River Group; Minnesota. *A*, Transverse section. *B*, *C*, Vertical sections, $^{14}/_{1}$ (after Ulrich).

walled, separated from one another by smaller angular mesopores, and containing cystiphragms. Acanthopores usually present. Ordovician.

Mesotrypa, Ulrich; Ordovician. *Aspidopora*, Ulrich; Ordovician and Silurian.

Family 2. **Heterotrypidae.** Ulrich.

Zoaria frondescent, ramose, or parasitic. Zoœcia polygonal, with moderately thin walls. Acanthopores present, sometimes of large size. Diaphragms numerous, horizontal. Cystiphragms wanting. Ordovician.

Dekayella, Ulrich (Fig. 454). Ramose, branches sometimes compressed. Mesopores more or less numerously distributed among the zoœcia. Acanthopores of two sizes, the smaller ones the more abundant, and present only in the peripheral region.

Dekayia, Ed. and H. (Fig. 455). Distinguished from *Dekayella* by the absence of the smaller set of acanthopores, and lesser number of mesopores and diaphragms.

Heterotrypa, Nich. (Fig. 185). Zoarium always frondescent, and acanthopores of small size only; otherwise like *Dekayella*. Abundant in Cincinnati Group.

Petigopora, Ulrich. Small parasitic species having strong acanthopores but no mesopores, and only a few diaphragms.

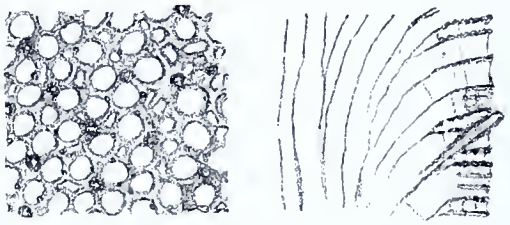

FIG. 454.

Dekayella obscura, Ulr. Cincinnati, Ohio. Tangential and vertical sections, $^{14}/_{1}$ (after Ulrich).

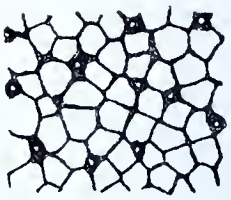

FIG. 455.

Dekayia aspera, Edw. and H. Cincinnati, O. Tangential section, $^{14}/_{1}$.

Family 3. **Calloporidae**. Ulrich.

Zoaria ramose, sub-frondescent, massive, or discoidal. Zoœcial apertures generally subcircular and separated more or less completely by angular mesopores; at other times polygonal, when the mesopores are few or wanting. Zoœcial tubes thin-walled, attaining their full size slowly. Acanthopores wanting. Ordovician to Devonian.

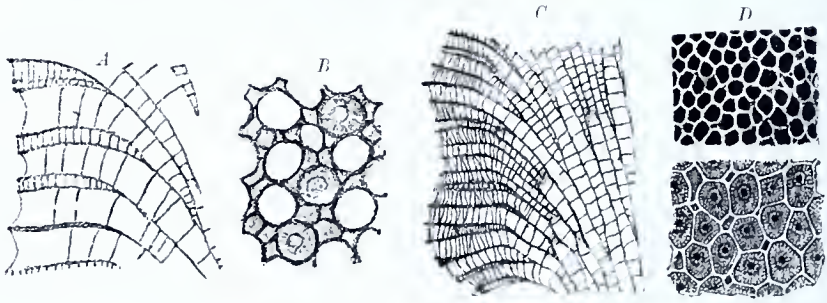

FIG. 456.

A, B, Callopora elegantula, Hall. Niagara; Indiana. Vertical and tangential sections, $^{14}/_{1}$. *C, D, C. multitabulata*, Ulr. Trenton; Minnesota. *C*, Vertical section, $^{7}/_{1}$. *D*, Surface having zoœcia open ($^{7}/_{1}$), and preserving zoœcial covers ($^{14}/_{1}$).

In this family the proximal ends of the tubes arising in the axial or "immature" region have the character of mesopores. The diaphragms are rather closely arranged in the tapering proximal end, then few or wanting for a considerable distance, and finally become crowded in the peripheral or mature region.

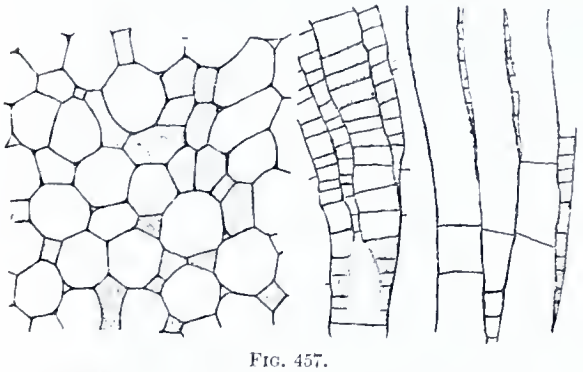

FIG. 457.

Diplotrypa Westoni, Ulr. Cincinnati Group; Manitoba. Tangential and vertical sections, $^{14}/_{1}$ (after Ulrich).

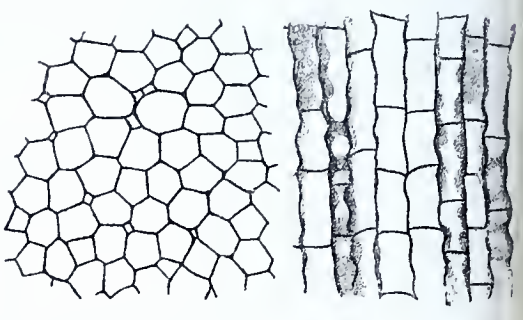

FIG. 458.

Monotrypa magna, Ulr. Lower Trenton; Illinois. Transverse and vertical sections, $^{7}/_{1}$ (after Ulrich).

Callopora, Hall (emend. Ulrich), (Fig. 456). Zoaria usually ramose and bushy, the branches often anastomosing. Apertures closed in the perfect state by perforated, often ornamented, covers, which are left behind, as growth proceeds, to form floors (diaphragms) of succeeding layers. Zoœcial tubes of two sizes in the axial region, the larger ones with six to eight sides, the smaller set four- or five-sided. Ordovician and Silurian.

Diplotrypa, Nich. emend. Ulrich (*Dianulites*, Zittel non Dybowski), (Fig. 457). Zoaria discoid, globular, or irregularly massive, generally free. Zoœcial tubes comparatively large, prismatic, with horizontal diaphragms. Mesopores few to numerous, varying in size. Ordovician.

Monotrypa, Nich. (*Dianulites*, Dyb. p.p.; *Ptychonema*, Hall), (Fig. 458). Distinguished from the preceding by the absence of mesopores and fewer diaphragms. Ordovician to Devonian.

Family 4. **Trematoporidae.** Ulrich.

Zoaria ramose or encrusting. Zoœcial tubes irregular in the axial region, their proximal ends with diaphragms, and usually constricted where the latter occur; walls thickened in the mature region, lines of contact distinct. Mesopores generally abundant, usually of large size, their apertures closed. Acanthopores more or less abundant. Ordovician.

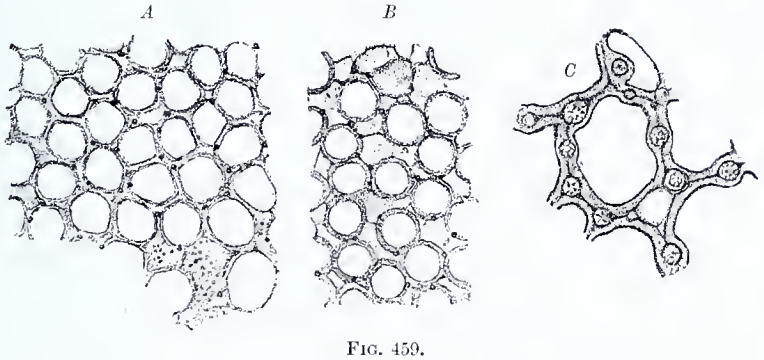

Fig. 459.

Tangential sections of *Batostoma* from the Lower Trenton of Minnesota. *A*, *B. fertile*, Ulr., $^{14}/_{1}$. *B*, Same, var. *circulare*, $^{14}/_{1}$. *C*, *B. Winchelli*, var. *spinulosum*, Ulr., $^{38}/_{1}$ (after Ulrich).

This family is principally distinguished from the *Calloporidae* by the presence of acanthopores and closed mesopores.

Batostoma, Ulrich (Fig. 459). Branches irregular, springing from a large basal expansion. Zoœcial walls of varying thickness, in contact only at limited points, and of two sizes in the axial region. Diaphragms strong, horizontal, complete. Species numerous and mostly very abundant.

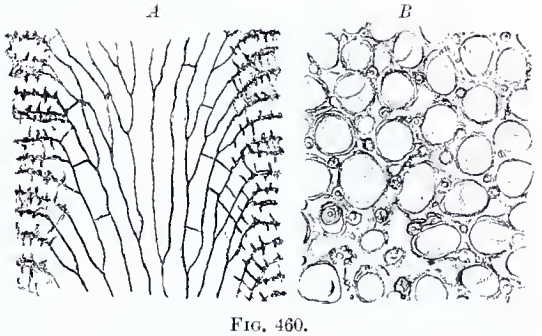

Fig. 460.

Hemiphragma irrasum, Ulr. Lower Trenton; Minnesota. *A*, Vertical section, $^{7}/_{1}$. *B*, Tangential, $^{14}/_{1}$ (after Ulrich).

Hemiphragma, Ulrich (Fig. 460). Like *Batostoma*, but diaphragms in peripheral part of tubes incomplete.

Trematopora, Hall (emend. Ulrich); *Stromatotrypa*, Ulrich.

Family 5. **Constellariidae.** Ulrich.

Zoaria ramose, frondescent, laminar, or encrusting. Zoœcial tubes thin-walled and prismatic in the axial region, thicker and sub-cylindrical in the peripheral; apertures rounded, the peristomes slightly elevated. Mesopores angular, abundant, generally isolating the zoœcia, at intervals gathered into usually stellate clusters; closed at the surface, the closure with numerous perforations. True acanthopores wanting, but small hollow spines or granules often very abundant. Diaphragms straight and complete in both sets of tubes. Ordovician and Silurian.

Constellaria, Dana (Fig. 461). Zoaria growing erect from a basal expansion which is attached to foreign bodies. Surface with depressed stellate maculae, the spaces between the rays elevated and occupied by two or three short rows or clusters of

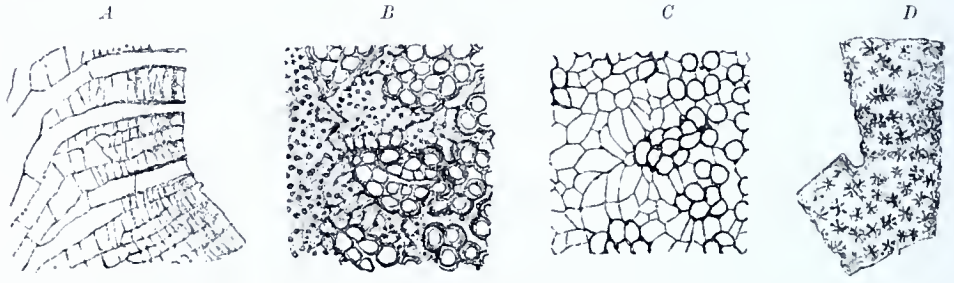

Fig. 461.

Constellaria florida, Ulr. Cincinnati, O. *A*, Vertical section. *B*, Tangential, showing aged condition. *C*, Average tangential section, all $^{14}/_{1}$. *D*, Branch of the natural size (after Ulrich).

closely approximated zoœcial apertures. Mesopores aggregated in the maculae, internally with gradually crowding diaphragms. Ordovician.

Stellipora, Hall (non Hagw. nec Haime). Differs from the above in its encrusting habit, and in having only mesopores in interspaces between the raised zoœcial clusters. Ordovician.

Nicholsonella, Ulrich (Fig. 462). Laminar expansions, sometimes giving off flattened, intertwining branches or fronds. Interzoœcial spaces wide, and with

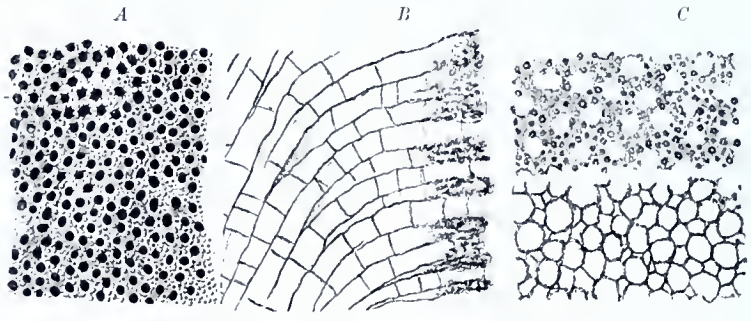

Fig. 462.

Nicholsonella pulchra, Ulr. Lower Trenton; Tennessee. *A*, Surface, $^{7}/_{1}$. *B*, Vertical section, $^{14}/_{1}$. *C*, Tangential sections at different levels, $^{14}/_{1}$ (after Ulrich).

numerous mesopores, which have thicker and more numerous diaphragms than the zoœcial tubes; the spaces become filled up with age by a calcareous deposit, rendering walls of mesopores unrecognisable. Ordovician.

Idiotrypa, Ulrich; (?) *Dittopora*, Dybowski. Silurian.

Family 6. **Batostomellidae.** Ulrich.

Zoaria usually ramose, occasionally sub-lobate, massive, laminar, or parasitic, often consisting of superimposed layers. Zoœcia with thick walls in the mature region, usually appearing here as fused. Diaphragms horizontal, those in peripheral region with central perforation. Acanthopores and mesopores usually present; the latter small, often intermittent. Ordovician to Permian.

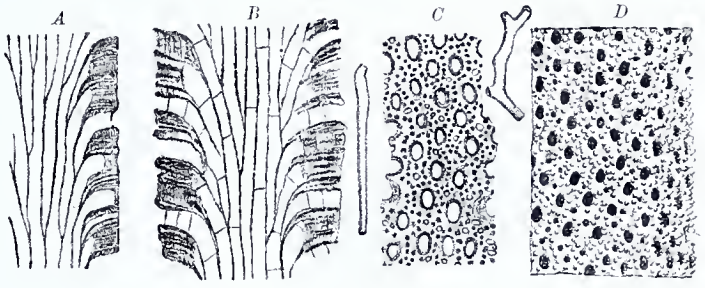

Fig. 463.

Batostomella spinulosa, Ulr. Chester Group; Kentucky. *A*, *B*, Vertical sections, one with and the other without diaphragms, $^{14}/_{1}$. *C*, Tangential section, $^{14}/_{1}$. *D*, Surface, $^{14}/_{1}$. On either side of *C* are branches of the natural size (after Ulrich).

Bythopora, Miller and Dyer. Small branching stems. Apertures oblique, attenuate above. Interspaces canaliculate, with an occasional mesopore or none. Ordovician.

Callotrypa, Hall; Silurian. *Eridotrypa*, Ulrich; Ordovician to Devonian.

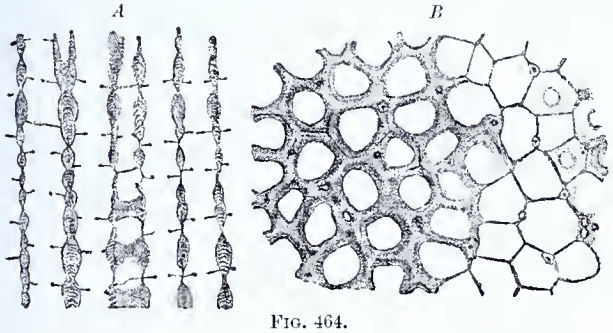

Fig. 464.

Stenopora americana, Ulr. Keokuk Group; Illinois. Vertical (*A*) and tangential (*B*) sections showing moniliform walls and perforated diaphragms, $^{14}/_{1}$ (after Ulrich).

Batostomella, Ulrich (*Geinitzella*, W. and W.; *Trematella*, Hall), (Fig. 463). Slender branches, without monticules. Apertures small, circular, or oval. Interspaces rounded or canaliculate, spinulose, the acanthopores small and usually very numerous. Mesopores small, sub-circular. Diaphragms few. Devonian to Permian.

Stenopora, Lonsd. (Fig. 464). Zoaria ramose, sub-lobate, massive, laminar, or parasitic. Surface even or montiferous. Zoœcial walls periodically thickened in the mature region. Large acanthopores at many of the angles between the zoœcia. Mesopores never very numerous, irregularly distributed. Diaphragms sometimes very scarce, but in most American species abundant in the peripheral region, and with a large central perforation. Sub-Carboniferous to Coal Measures.

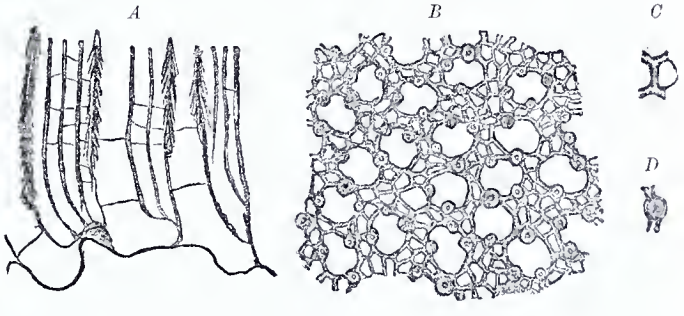

Fig. 465.

Lioclema foliata, Ulr. Keokuk Group; Illinois. *A*, Vertical section, $^{21}/_{1}$. *B*, Tangential section, $^{21}/_{1}$. *C*, Portion of wall and acanthopore, $^{38}/_{1}$ (after Ulrich).

Anisotrypa, Ulrich. Divisional line between adjoining tubes more sharply defined, and periodic swellings of the walls much less distinct than in *Stenopora*. Acanthopores and mesopores absent; perforated diaphragms numerous. Sub-Carboniferous.

? *Lioclema*, Ulrich (Fig. 465). Ordovician to Sub-Carboniferous.

Family 7. **Amplexoporidae.** Ulrich.

Zoaria ramose, encrusting, discoidal, or massive, rarely bifoliate. Zoœcial tubes comparatively simple, prismatic, with a well-marked divisional line between adjoining tubes. Mesopores practically absent, but small abortive cells sometimes found among the large zoœcia forming the monticules. Acanthopores generally abundant, sometimes wanting. Ordovician to Devonian.

Amplexopora, Ulrich. Zoaria ramose. Acanthopores always present, varying in size and number. Diaphragms complete, horizontal. Ordovician to Devonian.

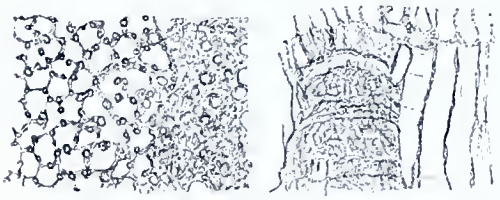

Fig. 466.

Atactopora maculata, Ulr. Cincinnati, O. Transverse and vertical sections, $^{14}/_{1}$, showing greater part of a solid macula (after Ulrich).

Monotrypella, Ulrich. Like the above, but without acanthopores. Ordovician to Devonian.

Petalotrypa, *Leptotrypa*, and *Discotrypa*, Ulrich. Ordovician to Devonian.

Atactopora, Ulrich (Fig. 466). Zoaria thin, growing on *Orthoceras*. Zoœcial apertures indented or floriform, according to position of the very numerous acanthopores. Rather large, solid elevations, composed of abortive cells, and completely filled by calcareous deposit, stud the surface at regular intervals. Diaphragms thin, few, sometimes wanting. Ordovician.

Sub-Order C. CRYPTOSTOMATA. Vine.

Primitive zoœcium short, pyriform to oblong, quadrate, or hexagonal, sometimes tubular, the aperture anterior. In the mature colony the aperture is concealed, occurring at the bottom of a tubular shaft ("vestibule"), which may be intersected by straight diaphragms or hemisepta, owing to the direct superimposition of layers of polypides. Vestibular shaft surrounded by vesicular tissue, or by a solid calcareous deposit; the external orifice rounded. Marsupia and avicularia wanting.

The *Cryptostomata* differ from the *Trepostomata* chiefly in that the "immature region" (primitive cell) is usually much shorter, and the passage to the mature region more abrupt.

Some of the *Cryptostomata* are ramose, and have long, thin-walled prismatic tubes in the axial region, with or without diaphragms, precisely as in the ramose *Trepostomata* and *Cyclostomata;* but they are distinguished from the latter by the presence of hemiscpta, similar to those occurring in the vestibule of *Escharopora* and *Phaenopora*, two of the most typical genera of the *Cryptostomata*. That these axial tubes are not of primary importance is shown by such genera as *Coelocnus*, *Rhombopora*, etc., in whose axial tubes a second layer of zoœcia has grown over the first. This is a rare condition, and is probably to be attributed to an accidental interruption of growth. But, where observable, it is to be noticed that the inner extremities of the zoœcia of the second layer are not drawn out into tubes like those of the primary set, but are short, and in all essential respects like those of *Escharopora*.[1]

The *Cryptostomata* are probably nothing more than Palaeozoic *Chilostomata*, differing, however, from the typical members of the latter (1) in having neither marsupia nor avicularia; (2) in the much greater deposit of calcareous matter upon the front of the zoœcia, thus producing the vestibule; (3) in that successive layers of polypides are often developed, one directly over the other, in a continuous tube; and (4) in that whenever a zoarium attains an uninterrupted width of more than 8 mm., it exhibits clusters of cells differing more or less, either in size or elevation, from the average zoœcia. The last two distinctions are suggestive of the *Trepostomata;* and the presence of a vestibule reminds us of certain Mesozoic and recent

[1] [The almost universal practice has been to accept the presence of tubular zoœcia as fully demonstrating the Cyclostomatous affinities of the species producing them. Recent investigations, however, show that the mere form of the zoœcium cannot be relied upon as a subordinal character any more than is the presence of tabulae in a tubular organism a certain indication of an Anthozoan.]

Chilostomata, which have the same tubular prolongation of the aperture. Thus, the recent *Adeonella atlantica*, Busk, has not only a vestibule, but hemisepta as well. Hemisepta are never found in the *Cyclostomata* and *Trepostomata*, but are a very common feature of the *Cryptostomata*. They occur at the bottom of the vestibule, and doubtless served as supports for the movable operculum.

Family 1. **Ptilodictyonidae.** Ulrich.

Zoaria bifoliate, composed of two layers of zoœcia grown together back to back, continuous or jointed, and forming leaf-like expansions, or compressed, branching, or inosculating stems. Mesial plates without median tubuli; hemisepta usually present. Inner orifice generally semi-elliptical, the outer more rounded, usually ovate, and surrounded by either a sloping area or a ring-like peristome. Vestibules separated by thick walls. Ordovician to Sub-Carboniferous.

Ptilodictya, Lonsd. (*Heterodictya*, Nich.) Zoaria simple, unbranched, lanceolate, or falciform, with a small basal expansion. In the young condition the zoarium consists of longitudinally arranged, narrow, oblong-quadrate zoœcia, new zoœcia, of different width and arrangement, being added subsequently on each side. In the vestibular or outer region the walls are more or less thickened, solid, and with a double row of exceedingly minute dots. Ordovician to Devonian.

Escharopora, Hall (*Nicholsonia*, Waag. and Wentz). Distinguished from the last chiefly by the arrangement of the zoœcial apertures, which are in diagonally intersecting series, and by the hexagonal sloping area which surrounds the external orifice. Ordovician.

Clathropora, Hall. Zoaria composed of anastomosing branches forming a regular network with round fenestrules, terminating below in a pointed, articulating base. Zoœcial apertures usually sub-quadrate, arranged longitudinally. Ordovician to Devonian.

Phaenopora, Hall. Zoaria as in *Ptilodictya*, except that there are two mesopores in each interspace between the ends of the zoœcial apertures. Ordovician and Silurian.

Arthropora, Ulrich. Zoaria bushy, spreading in a plane, composed of numerous equal segments. Zoœcial apertures elliptical, surrounded by a delicate peristome. Interspaces with one or more threadlike ridges, variously disposed, and with a row of minute papillae. Ordovician.

Graptodictya, *Ptilotrypa*, Ulrich; Ordovician. *Taeniodictya*, Ulrich; Devonian and Sub-Carboniferous.

Stictotrypa, Ulrich. Branches not jointed at the base. Zoœcial apertures circular or elliptical, with a distinct, evenly elevated peristome. Ordovician and Silurian.

Stictoporella, Ulrich. Zoaria variously formed, with elliptical apertures placed at the bottom of a sloping area. Thick-walled, untabulated mesopores occur between the zoœcial apertures and line the zoarial margins. Ordovician to Sub-Carboniferous.

Intrapora, *Coscinella*, Hall. Devonian.

Family 2. **Rhinidictyonidae.** Ulrich.

Zoaria bifoliate, continuous or jointed, forming compressed branches or leaf-like expansions; occasionally trifoliate. Primitive cells sub-quadrate, arranged longitudinally. Both primitive and superficial apertures elliptical or sub-circular, sometimes a little truncated posteriorly. Inferior hemiseptum and lunarium wanting. Median tubuli present between the median laminae, and between the longitudinal rows of zoœcial tubes. Mesopores absent, but vesicular tissue often present. Chiefly Ordovician.

Rhinidictya, Ulrich (*Stictopora*, Ulrich non Hall). Zoaria composed of narrow,

compressed, dichotomously dividing, straight-edged branches, attached to foreign bodies by a continuous expanded base. Ordovician and Silurian.

Eurydictya, *Dieranopora*, *Goniotrypa*, Ulrich. Ordovician.

Euspilopora, Ulrich. Small, irregularly divided branches, with serrated or wavy edges. Devonian.

Phyllodictya, Ulrich. Zoœcial tubes long, with complete diaphragms, but no hemisepta. Ordovician.

Pachydictya, *Trigonodictya*, Ulrich. Ordovician and Silurian.

Family 3. **Cystodictyonidae.** Ulrich.

Zoaria consisting of two or three layers of cells grown together back to back, forming branching, perforated, or entire leaf-like expansions, or triangular branches. Primitive cells semi-cordate or obovate-acuminate in outline, arranged longitudinally. Primitive aperture sub-circular, but becoming drawn out into a tubular vestibule as growth proceeds. Superficial aperture with peristome, and more or less well-developed lunarium. Interzoœcial spaces occupied by vesicular tissue, often filled with a calcareous deposit near the surface. Silurian to Carboniferous.

Cystodictya, Ulrich. Zoaria ramose, branches sharply elliptical, with sub-parallel, non-poriferous margins. Interapertural spaces finely striated, granulose or smooth; pits and cells showing only in a worn condition. Silurian to Carboniferous.

Coscinium, Keyser (*Coscinotrypa*, Hall); *Dichotrypa*, Ulrich. Silurian to Carboniferous.

Taeniopora, Nich. Distinguished from *Cystodictya* by having a longitudinal ridge or keel, which divides each face into two equal parts. Devonian.

Prismopora, *Scalaripora*, Hall. Devonian.

Evactinopora, Meek and Worth. Zoaria free, consisting of four or more vertical leaves arranged in a stellate or cruciform fashion. Sub-Carboniferous.

Glyptopora, Ulrich. Zoaria consisting of thin expansions traversed on both surfaces by salient ridges, or of uni-laminate bases on which the coalescing ridges of the upper surface are greatly developed and form large leaves. These ridges or leaves are composed of two layers of cells growing in opposite directions from a mesial lamina. Upper surface with solid maculae or "dimples." Sub-Carboniferous.

Rhinopora, Hall. Zoaria forming large undulating expansions, the free margins thickened or sharp and non-poriferous. Surface without maculae or monticules, but exhibiting thread-like bifurcating ridges, which appear as shallow grooves when the surface is worn. Large median tubuli between the mesial laminae. Silurian.

Family 4. **Arthrostylidae.** Ulrich.

Zoaria articulated, consisting of numerous sub-cylindrical segments united into small pinnate or bushy colonies, or of continuous, dichotomously divided branches. Zoœcia sub-tubular, more or less oblique, radially arranged about a central axis, and opening on all sides of the segments; or one side may be non-celluliferous and longitudinally striated. Ordovician and Silurian.

Arthrostylus, Ulrich. Zoaria bushy, dichotomously branching, the whole consisting of numerous exceedingly slender, equal, sub-quadrate segments, united by terminal articulation. Zoœcia usually arranged in three rows between longitudinal ridges; the fourth face with longitudinal striae only. Ordovician.

Helopora, Hall. Like the preceding, but the segments are larger, and have zoœcial apertures on all sides. Ordovician and Silurian.

Sceptropora, Ulrich. Segments short, greatly expanded above, celluliferous all around. Ordovician and Silurian.

Arthroclema, Bill. Segments sub-cylindrical, celluliferous on all sides, arranged pinnately. Articulation both terminal and lateral. Ordovician.

Nematopora, Ulrich. Zoaria very slender, ramose, continuous above the pointed basal extremity. Zoœcia sub-tubular, arranged radially about one or two minute axial tubes. Ordovician and Silurian.

Family 5. **Rhabdomesodontidae.** Vine.

Zoaria ramose or simple, not articulated, sometimes with a large or small axial tube, and generally solid. In the latter case the axial region is occupied by thin-walled primitive tubes, with or without diaphragms. Hemisepta usually present, but never conspicuous. External zoœcial apertures oval or circular, regularly arranged, and usually at the bottom of a rhombic or hexagonal sloping area, or between longitudinal ridges. Mesopores absent. Silurian to Carboniferous.

Rhombopora, Meek (*Orthopora*, Hall). Zoaria slender, ramose, solid. Zoœcial tubes with the outer or vestibular region thick-walled, apertures arranged in diagonal or longitudinal lines. Strong acanthopores and smaller spines generally present. Silurian to Carboniferous.

Bactropora, Hall. Zoaria simple or only slightly branched, the lower extremity pointed. Sub-Carboniferous.

Rhabdomeson, Young. Differs from *Rhombopora* only in having a slender axial tube, to which the proximal ends of the zoœcia are attached. Carboniferous.

Coeloconus, Ulrich. Zoaria simple, hollow, expanding gradually from the striated base ; substance thin. Primitive portion of zoœcia short, with well-developed hemisepta. Sub-Carboniferous.

? *Tropidopora*, Hall ; Devonian. (?) *Streblotrypa*, Ulrich ; Devonian and Sub-Carboniferous.

Family 6. **Fenestellidae.** King.

Zoaria forming reticulate expansions, celluliferous on one side only. They are composed of rigid branches united by regular non-poriferous bars (dissepiments) ; or may be sinuous and anastomose at regular intervals ; or may remain free. Zoœcia enclosed in a calcareous crust, which is minutely porous, especially on the non-celluliferous side. Primitive portion of zoœcia oblong, quadrate, or hexagonal in outline. Superior hemiseptum usually present, the inferior one less frequently. Primary orifice anterior, semi-elliptical, truncated behind. External apertures rounded, with peristome, and covered, when perfect, by centrally perforated closures. Ordovician to Permian.

The zoarial characters of the *Fenestellidae* are extremely constant, and are of the greatest systematic importance. The zoœcial cavity in this family is very similar to that of the *Ptilodictyonidae* and *Rhinidictyonidae ;* and the same is also true of both the primary and external orifices. Ulrich considers the family as having been derived from *Phylloporina*.

Fenestella, Lonsd. (*Fenestrella*, d'Orb. ; *Actinostoma*, Young), (Fig. 467). Zoaria flabellate or funnel-shaped, poriferous on the inner side. Branches generally straight, sometimes flexuous, connected at regular intervals by dissepiments. Zoœcia in two rows, separated by a plain or tuberculose median keel. Ordovician to Permian ; chiefly Devonian and Sub-Carboniferous.

Semicosminium, Prout (*Carinopora*, Nich.) Zoaria funnel-shaped, poriferous on the outer side. Dissepiments wide, very short, the branches appearing to anastomose on the non-poriferous face, where the fenestrules are sub-rhomboidal or rounded. Zoœcia in two ranges, median keel very high and expanded at the summit. Silurian and Devonian.

Fenestropora, Hall. Like the preceding, except that the reverse of the zoarium and the expanded summits of the carinae bear large, scattered pores or pits. Devonian.

Isotrypa, *Loculipora*, *Unitrypa*, Hall. Silurian and Devonian.

Hemitrypa, Phill. Differs from *Fenestella* in having a retieulated superstructure, whose meshes correspond in position and number with the zoœcial apertures in the

Fig. 467.

Fenestella retiformis, Schloth. Permian Dolomite; Pössneck, Thuringia. *A*, Fragment of zoarium, natural size. *B*, Portion of external surface, slightly enlarged. *C*, Magnified portion of interior celluliferous surface.

branches beneath. The structure rests on pillars which rise at regular intervals from the moderate median keel of the branches. Silurian and Devonian.

Helicopora, Claypole. Zoaria spiral, the inner edge thickened and non-poriferous, but not forming a solid axis. Otherwise like *Fenestella*. Silurian, (?) Devonian.

Archimedes, Lesueur (Fig. 468). Distinguished from *Helicopora* by its solid central

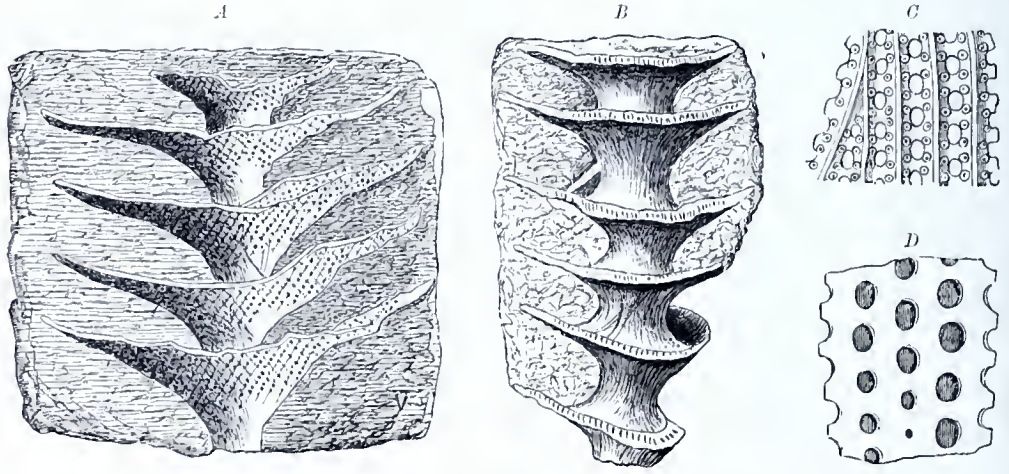

Fig. 468.

Archimedes Wortheni, Hall sp. Sub-Carboniferous; Warsaw, Ill. *A*, Fragment of well-preserved zoarium, $^1/_1$ (after Roemer). *B*, Broken spiral zoarium (after Quenstedt). *C*, Portion of interior or upper surface of the expansion, enlarged (after Roemer). *D*, External or inferior aspect of same (after Hall).

axis. As a rule, the fenestrated expansion is broken away, leaving only the screw-like axis. Sub-Carboniferous.

Lyropora, Hall. Zoaria flabellate, the fenestrated portion spread between the arms of a non-celluliferous U- or V-shaped support; free or pedunculate at the base. Zoœcia in from two to five rows. Sub-Carboniferous.

Fenestralia, Prout. Having a median keel as in *Fenestella*, but with four ranges of zoœcia instead of two. Sub-Carboniferous (St. Louis Group).

Polypora, M'Coy. Differs from *Fenestella* in having two to eight rows of cells on a branch, and in wanting a median keel. The latter is sometimes represented by a row of strong tubercles. Silurian to Carboniferous.

Thamniscus, King. Like *Polypora*, but branches bifurcating more freely, and with only a few dissepiments or none. Silurian to Permian.

Phyllopora, King. Zoaria funnel-shaped, celluliferous on the outer side, and consisting of anastomosing branches, which form a regular, round-meshed network. Zoœcia in two or more rows. Devonian and Permian.

Ptiloporella, *Ptiloporina*, Hall. Silurian and Devonian.

Ptilopora, M'Coy (*Dendricopora*, de Kon.) Zoaria pinnate, the central branch much stronger than the oblique lateral branches, which are united by dissepiments. Zoœcia in two ranges. Devonian and Sub-Carboniferous.

Family 7. **Acanthocladiidae.** Zittel.

Zoaria poriferous on one side only, pinnate or forming fenestrated expansion; consisting of strong, central stems which give off numerous, smaller, lateral branches from their opposite margins. The lateral branches are free or unite with those of the next stem. Non-poriferous dissepiments absent. Zoœcial characters mostly as in the Fenestellidae. Silurian to Permian.

Pinnatopora, Vine (*Glauconeme*, auct.) Zoaria small, delicate, with short, free, lateral branches given off frequently at regular intervals. Cells in two rows, one on each side of a moderate median keel. Silurian to Carboniferous.

Septopora, Prout. Zoaria fenestrated, flabellate, or leaf-like. Primary branches numerous, increasing by bifurcation or interpolation; the lateral branches uniting with those of adjacent stems. Reverse usually with fine striae and scattered dimorphic pores. Celluliferous side with two rows of zoœcia arranged as in *Pinnatopora*. Chester Group and Coal Measures.

Acanthocladia, King. Like *Pinnatopora*, but larger, stronger, and with three or more ranges of cells. Coal Measures and Permian.

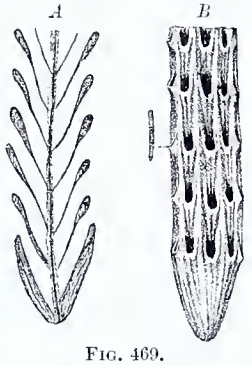

Fig. 469.

Helopora spiniformis, Ulr. Trenton; Tennessee. *A*, Vertical section, $^{14}/_{1}$. *B*, Segment, $^{1}/_{1}$ and $^{14}/_{1}$ (after Ulrich).

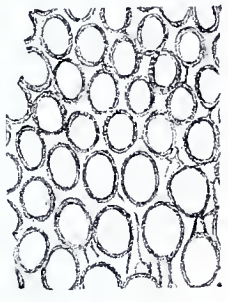

Fig. 470.

Pachydictya foliata, Ulr. Lower Trenton; Minnesota. Tangential section, $^{14}/_{1}$ (after Ulrich).

Synocladia, King. Differs from *Septopora* in the same manner as the preceding differs from *Pinnatopora*. Permian.

Diplopora, Young. Essentially a *Pinnatopora* without lateral branchlets. Carboniferous.

Ichthyorachis, M'Coy, *Pennirctepora*, d'Orb., and *Ramipora*, Toula, may belong here.

Family 8. **Phylloporinidae.** Ulrich.

Zoaria branching, celluliferous on one side only, the other side striated; branches free or anastomosing. Zoœcia more or less tubular, often with diaphragms. Hemisepta wanting. Ordovician to Coal Measures.

Phylloporina, Ulrich. Branches irregularly anastomosing, with two to eight ranges of zoœcia on the celluliferous side. Tabulated interstitial spaces generally present, closed at the surface. Ordovician and Silurian.

Drymotrypa, Ulrich; Ordovician and Silurian. *Chainodictyon*, Foerste; Coal Measures.

The following genera of doubtful affinities may be provisionally appended here:—*Proutella*, *Cycloporella*, *Worthenopora*, Ulrich; *Cyclopora*, Prout; *Paleschara*, Hall.

Sub-Order D. CHILOSTOMATA. Busk.

(*Bryozoaires cellulinés*, d'Orbigny.)

Zoœcia oval, turbinate, urceolate, quadrate, or hexagonal, arranged usually side by side. Orifice more or less anterior, of smaller diameter than the zoœcium, closed by a movable cover. Ova commonly matured in external marsupia. Appendicular organs frequently present.

True *Chilostomata* are first met with in the Jura, but their progenitors are undoubtedly to be looked for in the Palaeozoic *Cryptostomata*. They attain an astonishing development in the Upper Cretaceous, and in the Tertiaries and existing seas they greatly surpass the *Cyclostomata* in number and variety of species.

Not all of the *Chilostomata* have a completely calcified zoarium, some being corneous and flexible (*Flustridae*), and others having the front wall of the zoœcia more or less membraneous and the rest calcareous (*Membraniporidae*). Consequently, in fossil examples of the latter, the zoœcia are entirely open on the upper or front side (Fig. 477). Avicularia and vibracula are very commonly present, and are indicated in fossils by the "special pores" in which they were lodged. External ovicells are more commonly developed than in the *Cyclostomata*, and usually occur as rounded, blister-like cavities in front of the zoœcial apertures. Reproduction by gemmation takes place at the growing edge of the colony, the young cells arising from the anterior end or from either side of the parent cell; and repeated gemmation almost always results in a more or less regular arrangement in series. Direct communication between adjoining zoœcia is effected by means of small perforated plates (*communication plates, Rosettenplatten*), set in corresponding positions in the side walls of each zoœcium.

The classification of the *Chilostomata* is as yet in an unsettled condition. The older systems of d'Orbigny and Busk were highly artificial, undue prominence having been given to zoarial modifications; but through the labours of Smitt, Hincks, and Waters, who have demonstrated the much greater importance of zoœcial characters, a decided advance has been made. Only brief descriptions of the more important genera, or those having numerous fossil representatives, can be introduced here.

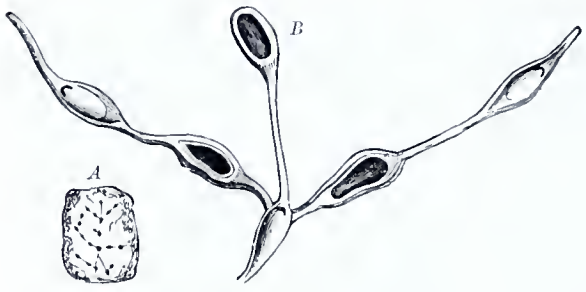

Fig. 471.

Eucratea labiata, Novak sp. Cenomanian; Velim, Bohemia. *A*, Zoarium, 1/1. *B*, Zoœcia, three of them with fractured walls, highly magnified (after Novak).

Family 1. **Eucrateidae.** Busk.

Zoaria branching, erect, and free, or recumbent. Zoœcia uniserial or biserial, pyriform, with a sub-terminal and usually oblique aperture. Avicularian and vibracular appendages wanting. Cretaceous to Recent.

Eucratea, Lamx. (Fig. 471). Zoaria entirely decumbent, or composed of a creeping, adherent base and erect branching shoots. Zoœcia calcareous or subcalcareous, rising one from another so as to form single series. Branches springing from the front of a zoœcium below the aperture.

Family 2. **Cellulariidae.** Busk.

Zoarium erect, usually jointed, dichotomously branching, phytoid. Zoœcia in two or more series, closely united and arranged in the same plane. Sessile avicularia and vibracula generally present. Tertiary and Recent.

Cellularia, Pallas; *Menipea, Caberea*, Lamx.; *Scrupocellaria*, Van Bened. Miocene to Recent.

Family 3. **Gemellariidae.** Busk.

Zoarium sub-calcareous, flexible, continuous. Zoœcia somewhat obconical, opposite, usually in pairs, unarmed. Recent.

Gemellaria, Savigny ; *Scruparia*, Hincks ; *Notamia*, Fleming.

Family 4. **Cellariidae.** Hincks (*Salicornariadae*, Busk.)

Zoarium erect, sub-cylindrical, dichotomously branching, usually jointed. Zoœcia rhomboidal or hexagonal, each corresponding to an area, and disposed in series about an imaginary axis ; front depressed, usually concave. Orifice crescentic or semi-circular, situated slightly above the centre of the cell. Oœcia inconspicuous, opening at or near the summit of the area above the orifice. Avicularia usually present. Cretaceous to Recent.

Cellaria, Lam. (*Salicornaria*, Cuv. ; *Salicornia*, Schweigg), (Fig. 472). Zoarium jointed, the segments sub-cylindrical and connected by flexible, horny tubes. Zoœcia immersed, surrounded by a raised border, disposed in quincunx. Avicularia irregularly distributed, situated above a cell, or occupying the place of one.

Fig. 472.

Cellaria rhombifera, Goldf. sp. Oligocene ; Kaufungen, near Cassel. Enlarged (after Reuss).

Family 5. **Selenariidae.** Busk.

Zoaria circular or irregular in outline, the celluliferous side convex, the lower concave or flat, probably free in the mature condition. Upper surface arcolated, the zoœcia immersed,

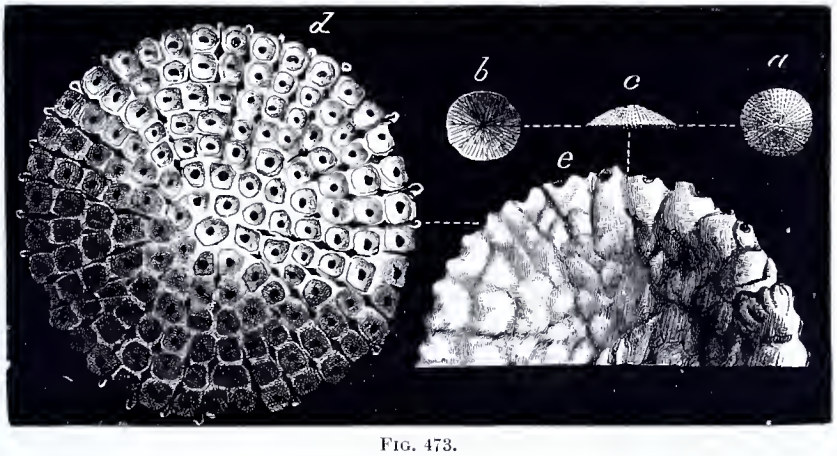

Fig. 473.

Lunulites Goldfussi, Hagw. Upper Cretaceous, Lüneburg. *a-c*, Zoarium of the natural size ; *d*, Upper surface, enlarged ; *e*, Lower surface, enlarged.

their borders elevated. Orifice rounded or semi-elliptical, situated more or less in advance of the depressed front. Small vibracular cells usually present. Cretaceous to Recent.

Lunulites, Lamx. (Fig. 473). Zoœcia arranged in series radiating from the centre and bifurcating as they advance toward the border. Vibracular cells usually elongate, lying in linear series between the rows of zoœcia. Very abundant in the Upper Cretaceous and Tertiary ; also Recent.

Stichopora, Hagw. emend. Busk. Vibracular cells wanting. Zoœcia equal, hexagonal, not arranged in radiating series. Cretaceous.

Selenaria, Busk. Cretaceous to Recent.

Family 6. **Onychocellidae.** Jullien, emend.

Zoaria encrusting or erect, ramose, continuous, the branches more or less compressed and bilaminar; surface areolated. Zoœcia usually hexagonal, their margins raised, the front not entirely calcified. Opesial aperture of moderate size, generally semi-elliptical, sometimes spreading below, in other cases sub-circular. Oral opening small, usually crescentic or semi-circular. Oœcia inconspicuous; interealated vicarious avicularia generally present; special pores wanting. Cretaceous to Recent; chiefly Cretaceous.

Fig. 474.

Onychocella angulosa, Reuss sp. Upper Eocene; Northern Italy. Surface, $^{20}/_{1}$ (after Waters).

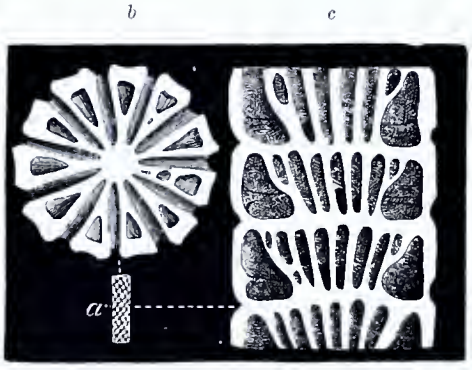

Fig. 475.

Vincularia virgo, Hagw. Upper Cretaceous; Rugen. *a*, Portion of zoarium, $^{1}/_{1}$; *b*, Cross-section; *c*, Vertical section, enlarged.

According as the specimens were encrusting or erect, they have been called *Cellepora* and *Membranipora*; or by others, *Eschara*, *Vincularia* (Fig. 475), and *Biflustra*. Indeed, according to Waters and others, all of these names have been applied to a single species, *Onychocella angulosa*, Reuss sp. The zoœcial characters are comparatively simple and uniform, and in most cases the same as in the *Cellariidae*. On the other hand, species having a larger opesial opening than usual (*Vibracella*, etc.) evince a decided resemblance to certain of the *Membraniporidae*. The systematic position of the family therefore appears to be intermediate between the *Cellariidae* and *Membraniporidae*. The relations of this family with the Palaeozoic *Cryptostomata* and *Trepostomata* are worthy of further investigation.

Onychocella (Jullien), Waters (*Eschara*, *Flustrellaria*, p.p., d'Orb.; *Cellepora*, *Membranipora*, *Vincularia*, etc., auct.), (Fig. 474). Zoaria encrusting or erect. Oral opening semi-circular or crescentic. Avicularian openings simple, oval; the area in which they are situated drawn out above. Cretaceous to Recent.

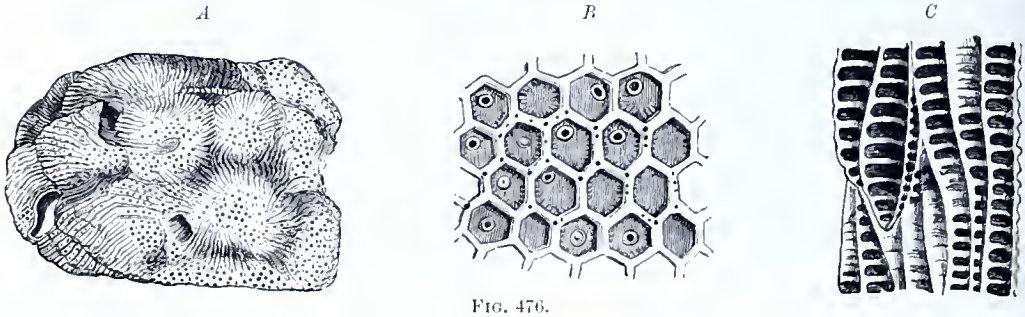

Fig. 476.

Cumulipora angulata, Munst. Oligocene; Doberg, near Bünde. *A*, Zoarium, natural size. *B*, Upper surface, enlarged. *C*, Vertical section, enlarged (after Reuss).

Vibracella, Waters (*Flustrellaria*, p.p., d'Orb.) Differs from *Onychocella* in having a larger aperture, which is often somewhat expanded below, and having vibracular cells instead of avicularia. Cretaceous and Tertiary.

? Cumulipora, Münst. (Fig. 476). Zoaria irregularly massive. Zoœcia partly recumbent, partly erect, and placed one above the other, so that they appear to form tabulated tubes. Tertiary.

Family 7. **Membraniporidae.** Busk.

Zoarium calcareous or membrano-calcareous, encrusting or erect, in the latter case bifoliate, or sub-cylindrical. Zoœcia placed side by side, and forming an irregular continuous expansion, or in linear series. Margins raised, the depressed front more or less membraneous. Cretaceous to Recent.

Membranipora, Blainv. (? *Marginaria*, Roemer ; (?) *Dermatopora*, Hagw.), (Figs. 477, 478). Zoaria encrusting, calcareous, or sub-calcareous. Zoœcia arranged irregularly or in rows, without a calcareous lamina on the front, or only partially covered by one, leaving a variously shaped aperture.

Family 8. **Cribrilinidae.** Hincks.

Zoaria encrusting or erect. Zoœcia having the front wall more or less fissured, or traversed by radiating furrows. Cretaceous to Recent.

Membraniporella, Smitt (Fig. 479). Zoaria encrusting or rising into free foliaceous

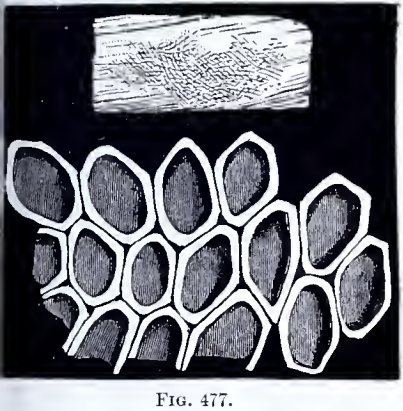

Fig. 477.

Encrusting zoarium of *Membranipora*, with non-calcified zoœcial walls. Magnified.

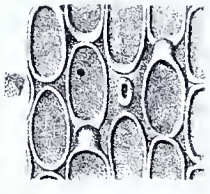

Fig. 478.

Membranipora plebeia, G. and H. Cretaceous ; N. J. Several cells highly magnified (after Gabb and Horn).

Fig. 479.

Membraniporella Abbotti, G. and H. sp. Cretaceous ; N. J. Zoœcia highly magnified (after Gabb and Horn).

Fig. 480.

Cribrilina Heermanni, G. and H. sp. Post-Pliocene ; Santa Barbara Co., Cal. Zoœcia highly magnified (after Gabb and Horn).

expansions, sometimes consisting of superimposed layers. Zoœcia closed in front by a number of flattened calcareous ribs more or less consolidated centrally. Cretaceous to Recent.

Cribrilina, Gray (Fig. 480). Zoaria usually encrusting. Zoœcia having the front more or less occupied by radiating or transverse rows of punctures, each row in a furrow ; orifice semi-circular or sub-orbicular. Cretaceous to Recent.

Fig. 481.

Micropora disparilis, G. and H. sp. Post-Pliocene ; Santa Barbara Co., Cal. Zoœcia highly magnified (after Gabb and Horn).

Family 9. **Microporidae.** Smitt.

Zoœcia having the front wall entirely calcareous ; usually with short, elevated margins, fissures, or perforations. Cretaceous to Recent.

Micropora, Gray (Fig. 481). Zoaria encrusting. Zoœcia with prominent raised margins ; the front depressed, with a perforation at each upper angle below the semi-circular or rounded orifice. Cretaceous to Recent.

Steganoporella, Smitt ; *Setosella*, Hincks. Recent.

Family 10. **Microporellidae.** Hincks.

Zoaria encrusting or erect, foliated or dendroid. Zoœcial orifice more or less semi-circular, with the lower margin entire; a crescentic or circular pore on the front wall usually just beneath the orifice. Cretaceous to Recent.

Fig. 482.

Microporella rudis, Reuss sp. Oligocene; Söllingen. Upper surface, enlarged.

Microporella, Hincks (Fig. 482). Zoarium encrusting or erect, bilaminar. Margin of zoœcia not elevated. Orifice with a straight, entire lower border, frequently with oval spines. Usually one semi-lunate or circular pore beneath the orifice, occasionally two or three. Tertiary and Recent.

Diporula, *Chorizopora*, Hincks. Tertiary and Recent.

? Monoporella, Hincks. Like *Microporella*, but without special pores. Cretaceous to Recent.

Family 11. **Porinidae.** d'Orbigny, emend. Hincks.

Zoaria encrusting, or erect and ramified. Zoœcia with a raised tubular or sub-tubular orifice, and frequently with a special pore on the front wall. Cretaceous to Recent.

Porina, d'Orb. Zoaria consisting of flattened or sub-cylindrical branches, celluliferous on both sides, or encrusting. With age the spaces between the raised apertures become filled with a porous calcareous deposit. Avicularia and oœcia occasionally distinguishable. Cretaceous to Recent.

Celleporella, Gray; *Anarthropora*, Smitt; *Lagenipora*, Hincks. Recent.

Family 12. **Escharidae.** Hincks.

Zoaria erect, unilaminate or bilaminate, foliaceous or ramose, or crustaceous, loosely attached or adnate. Zoœcia urceolate, the front entirely calcified, without raised margins. Orifice anterior, sub-circular to horseshoe-shaped, the lower border straight, broadly sinuate, or notched. An elevated secondary orifice, with the lower margin dentate, channeled, or enclosing an avicularium, often present, but no special pores. Cretaceous to Recent.

This family embraces a large number of fossil and existing Bryozoans, and in its present state can hardly be said to form a natural group. It is here that the much greater importance of zoœcial characters as compared with zoarial are particularly apparent; inasmuch as one genus, or in many cases a species, as now generally understood, may include a considerable range of zoarial types. To the palaeontologist the group offers exceptional difficulties, since generic characters frequently depend upon easily abraded or obscure modifications of the orifice.

Lepralia, Johnston (Fig. 483). Zoaria encrusting or rising into simple or branching expansions, composed of one or two layers of cells. Zoœcia usually ovate, the orifice with a thin peristome and entire lower margin. Rare in Cretaceous, more abundant in Tertiary and Recent.

Porella, Gray. Zoaria encrusting or erect. Zoœcia with a semi-circular primary orifice; the secondary (adult) orifice elongate, inversely sub-triangular, or horseshoe-shaped, and enclosing an avicularium with a rounded or sub-triangular mandible. Tertiary and Recent.

Smittia, Hincks. Zoaria encrusting, or erect and foliaceous. Primary orifice of zoœcia sub-orbicular, the lower margin with an internal median denticle. Secondary orifice canaliculate below; generally a small avicularium either within or just beneath the sinus. Miocene and Recent.

Mucronella, Hincks (Fig. 484). Similar to *Smittia*, but with simpler orifice, and

the lower part of the peristome elevated into a more or less prominent mucro. Tertiary and Recent.

Schizoporella, Hincks. Zoaria variable; zoœcial orifice varying from semi-circular to sub-orbicular, the lower margin with a distinct sinus. Cretaceous to Recent.

Fig. 483.

Lepralia pallasiana, Moll. Recent; England. Zoœcia highly magnified (after Hincks).

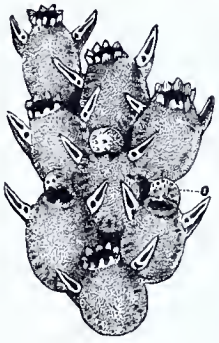

Fig. 484.

Mucronella coccinea, Abildg. Miocene; Eisenstadt, Hungary. A number of zoœcia enlarged (after Reuss). The apertures are denticulated, and each zoœcium has a pair of avicularia. *o*, Ovicell.

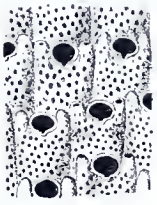

Fig. 485.

Schizoporella cornuta, G. and H. sp. Post-Pliocene; Santa Barbara Co., Cal. Zoœcia highly magnified (after Gabb and Horn).

Retepora, Imperato (*Phidolophora*, Gabb and Horn), (Fig. 486). Zoaria consisting usually of inosculating branches which spring from an encrusting base. Zoœcia disposed on one face of the branches only, in most cases immersed. Primary orifice rounded or semi-elliptical with entire border. Afterwards the peristome becomes much

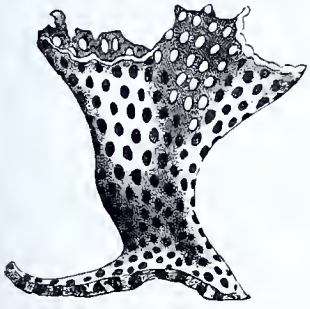

Fig. 486.

Retepora cellulosa, Linn. Crag; Suffolk, England.

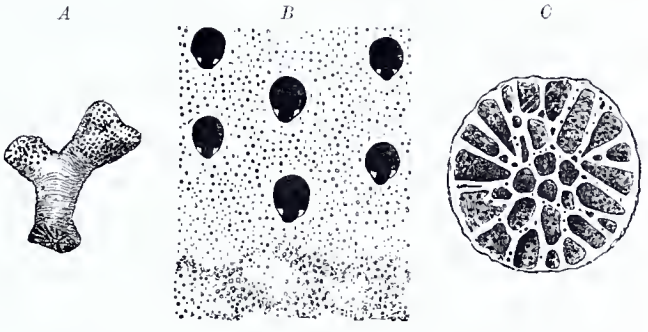

Fig. 487.

Myriozoum punctatum, Phill. sp. Miocene; Ortenburg, Bavaria. *A*, Zoarium, $^1/_1$. *B*, Upper surface, enlarged. In the forward portion the apertures are open, in the rear, covered over by a calcareous deposit. *C*, Cross-section of a branch.

raised and multiform; usually there is a fissure below, or there may be a prominent rostrum bearing an avicularium. Tertiary and Recent.

? *Myriozoum*, Donati (*Myriopora*, Blv.; *Vaginopora*, Reuss), (Fig. 487). Zoaria consisting of thick, dichotomously dividing branches, obtuse at their growing extremities, and rising from an attached basal expansion. Zoœcia disposed about an imaginary axis, even at the surface, their boundaries scarcely distinguishable. Entire surface and also the inner walls minutely porous. Orifice above the centre of the zoœcium, sub-orbicular, notched, or canaliculate below. As a rule, the openings are closed on the lower parts of the branches by a calcareous pellicle. Tertiary and Recent; perhaps also Cretaceous.

Family 13. **Celleporidae.** Busk.

Zoœcia urceolate, more or less erect, and irregularly crowded together; often forming several or many superimposed layers. Tertiary and Recent.

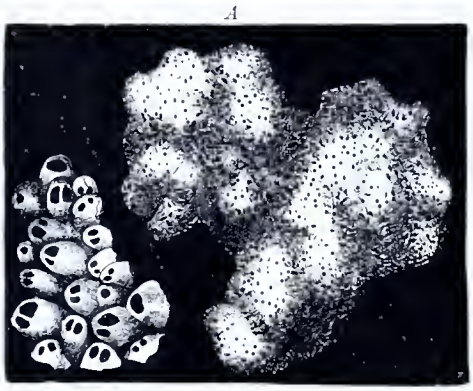

FIG. 488.

Cellepora conglomerata, Goldf. Oligocene; Astrupp, near Osnabrück. *A*, Zoarium, 1/1. *B*, Upper surface, enlarged.

Cellepora, Fabricius emend. Busk (*Spongites*, Oken; *Celleporaria*, Lamx.), (Fig. 488). Zoarium multiform, encrusting, or erect and ramose. Zoœcia in the older portions more or less erect and very irregularly disposed. Orifice terminal, entire, or sinuated, with or without internal denticles; in connection with it are usually one or more rostra bearing avicularia. Intercalated avicularia generally present also. The surface of weathered specimens dotted by the unequal apertures of vesicle-like cells. Tertiary and Recent.

Range and Distribution of the Bryozoa.

The class *Bryozoa* begins in the Ordovician, and is represented continuously up to the present time. The older Palaeozoic forms belong chiefly to two sub-orders—the *Cyclostomata* and *Trepostomata*.

A considerable number of *Cyclostomatous* genera are present in the Ordovician, all of them being closely related with Mesozoic and recent types; but throughout the remainder of the Palaeozoic, and in the Trias also, the sub-order is very sparingly represented (if we except the somewhat doubtful *Ceramoporidae* and *Fistuliporidae*), and in some parts quite absent. In the Jura and Cretaceous, however, a remarkable increase took place, hundreds of species being known from these formations. During the Tertiary their strength was again materially reduced, and the living *Cyclostomata* barely exceed 100 species in number.

The *Trepostomata* appear suddenly and in great variety in the Ordovician, from which over 200 species are known, but entered almost immediately upon a period of decline. From the Trenton and Cincinnati groups alone more species have been described than from all of the later Palaeozoic formations put together. There is at present no evidence to show that the group survived later than the Palaeozoic era, but it is not unlikely that their descendants may be found among certain Mesozoic families, such as the *Ceidae* and *Meliceritidae*, which are provisionally assigned to the *Cyclostomata*.

The *Cryptostomata* are likewise confined to rocks of Palaeozoic age, but, as has been remarked above, may be very confidently regarded as the forerunners of the *Chilostomata*. True members of the latter group are first met with in the Jura, but they develop rapidly, and from the Cretaceous onward remain the dominant type.

The Triassic and Liassic Bryozoans belong chiefly to the *Cerioporidae*. This family, together with the *Diastoporidae*, *Fascigeridae*, and other members of the *Cyclostomata*, are abundantly represented in the Middle Jura of Lorraine, Southern Germany, England, and Normandy. The Upper Jura, on the contrary, yields comparatively few Bryozoan fossils.

The *Cyclostomata* still predominate in the Neocomian and Gault, but in the Cenomanian a number of *Chilostomatous* genera make their appearance. The fauna

is especially well developed in the vicinity of Le Mans, Havre, and Essen, and in Saxony, Northern Germany, and Bohemia.

Bryozoans are surprisingly abundant in the Upper Cretaceous, particularly in the Upper Pläner of Northern Germany, Saxony, and Bohemia, in the White Chalk, and the facies of Aix-la-Chapelle and Maestricht. d'Orbigny alone has described not less than 547 species of Upper Cretaceous *Cyclostomata*, and about 300 *Chilostomata*.

The *Chilostomata* retain their supremacy throughout the Tertiary period. The Eocene and Oligocene deposits of the northern and southern slopes of the Alps are remarkable for the abundance of their Bryozoan remains; some of the most noted Eocene localities being Kressenberg, Hammer, and Neubeuern in Upper Bavaria; Mossano, Crosara, and Priabona, near Vicenza; and Oberburg in Styria. The Oligocene of Northern Germany, and the Miocene of Touraine, the Rhone Valley, Upper Swabia, and the Vienna Basin, are also remarkably rich in Bryozoan remains. The Pliocene fauna of Italy, Rhodes, Cyprus, and England (notably the Coralline Crag), is made up almost entirely of existing genera, and in many cases of existing species.

[The entire systematic portion of the preceding Bryozoan chapter has been prepared for the present edition by Mr. E. O. Ulrich, whose important researches in this and other departments of invertebrate palaeontology are familiar to all students of the science.—TRANS.]

Class 2. BRACHIOPODA. Cuvier. Duméril.[1]

Bivalved Molluscoidea with inequivalved, equilateral shells attached to extraneous objects by a posterior prolongation of the body, or pedicle, throughout life or during only

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a portion of their existence, or cemented ventrally. Valves ventral and dorsal. In composition, phosphatic or calcareous or both. Animal consisting of two pallial membranes intimately related to the shell. Within the mantle cavity at the sides of the mouth are inserted the two, more or less long, oral, usually spirally enrolled, cirrated brachia, which are variously modified, and are supported in the two terminal superfamilies by an internal calcareous skeleton, or brachidium, attached to the dorsal valve. Anus present or absent. Central nervous system consisting of an oesophageal ring with weakly developed brain and infra-oesophageal ganglionic swellings. Blood-vascular system probably present with the sinuses developed into vascular dilatations at the back of the stomach and elsewhere. Sexes separate. Exclusively marine.

The class appeared in the Lower Cambrian, attained its maximum development in the Silurian and Devonian, and is represented by about 140 living species. Probably upwards of 6000 fossil and recent species have been developed; these are distributed in 322 genera, grouped in thirty-one families, ten superfamilies, and four orders.

Cuvier (1792 and 1802) was the first to distinguish the Brachiopods from the *Acephala*, and created for them a fourth family in his class of Molluscs. To Duméril (1806) we owe the now generally accepted class name *Brachiopoda*, or arm-footed animals. Since the arms, or brachia, are not homologous with the foot of Molluscs, Gray (1821) changed the name to *Spirobranchiopoda;* Blainville (1824) to *Palliobranchiata;* Risso (1826) to *Branchiopoda;* Broderip (1839) to *Brachiopodidae;* Agassiz (1847) to *Branchionopoda;* Bronn (1862) to *Brachionocephala;* Paetel (1875) to *Branchionobranchia;* and Haeckel to *Spirobranchia*. None of these has displaced Duméril's term, though founded on a false physiological interpretation of the brachia.

External Characters: *Form.*—The shells of Brachiopods are very variable in form. Usually both valves are convex, but they may be nearly flat, with the interior cavity extremely shallow, or the dorsal valve may be concave and follow closely the curvature of the convex ventral valve. The ventral valve may be cone-shaped, with the dorsal operculiform, or the former may be so modified by cementation as to assume the appearance of a Cyathophylloid coral. The shell is commonly rostrate, with the ventral beak, or apex, more or less incurved over that of the dorsal valve, or the valves may be very greatly extended transversely. In fact, the form of the shell of Brachiopods is so variable that, as a rule, no greater value than specific can be attached to this feature.

Fixation.—The animal is generally attached to extraneous objects by a muscular pedicle which projects either from between the contracted posterior margin of the two valves (Fig. 499, *A*), through an opening in or under the beak (Fig. 498, *B*), or through the ventral valve (Fig. 512, *A*). With increasing age, however, the pedicle opening frequently becomes closed, and the pedicle itself atrophied. The animal may then be anchored by spines (*Choncles*, *Productus*) or be cemented by the whole or a part of the surface of the ventral valve (*Crania*, *Davidsonia*, *Thecidea*, *Streptorhynchus*). In some cases (*Glottidia* and *Lingula*) Brachiopods live throughout life partially buried in the sand or mud of the sea-bottom.

Ornamentation.—The external form and ornamentation of the shell afford important characters for determining the species. The anterior margin of one valve is frequently indented by a *median sinus*, and the other usually exhibits a corresponding *fold*, or elevation.

In the earliest shell growth stages Brachiopod shells are invariably smooth, and may remain so throughout life, but the greater number develop radial striae, ribs, or undulations, and these are usually crossed by concentric growth lines, or lamellae, which are sometimes of great width, or may be extended into spines. There may be more or less long tubular spines scattered over one or both valves, or sometimes restricted to a single row along the cardinal line. Under the term *Loricatae*, Leopold von Buch included all Brachiopods in which the radial folds, or costae, are arranged in regular succession in such manner that elevated ridges at the anterior margin of one valve coincide with the indentations of the other. In the *Biplicatae*, a median fold or sinus is bordered on either side by a broad fold. In the *Cinctae*, the plications of the two valves meet at the anterior margin in such manner as to form a straight instead of a crenulated line, as in the *Biplicatae*. In young specimens the ribs and folds are less prominent and numerous than at maturity. In very old or senile individuals the shell is usually thickened and obese, and the growth lines are much crowded anteriorly. At this stage old specific characters are seen to disappear, and at the same time new ones may be introduced.

Shell structure.—The test of Brachiopods is composed of laminae of various structure and composition, but differs considerably from that of Molluscs. The shell may be wholly calcareous or alternately calcareous and corneous. When entirely calcareous the laminae are never more than three in number: an inner thick prismatic layer, an intermediate laminar layer, and an outer epidermal film. The inner layer is made up of flattened prisms of calcite arranged parallel to one another with great regularity, and forming an acute angle with the surface of the shell (Fig. 489). In the *Thecidiidae* these fibrous prisms are so intimately united with one another that the shell substance appears almost homogeneous. Very often the fibrous layer is perforated by a series of minute canals which pass from one surface of the valve to the other in a more or less vertical direction, and are somewhat dilated externally. These canals contain tubuli, or certain prolongations derived from the mantle, but never communicate with the exterior, owing to the fact that the laminar layer of the shell is always covered with a chitinous epidermis (*periostracum*). With the aid of a magnifier the openings of these canals are visible in fossil forms, and they may be also seen in recent specimens after the epidermis has been removed by an application of caustic potash (Fig. 490). According to the presence

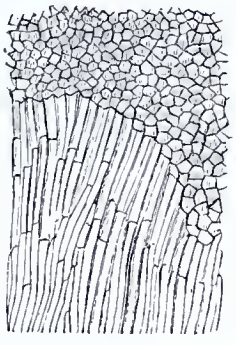


Fig. 489.

Prismatic fibrous structure of shell of *Rhynchonella* (*Hemithyris*) *psittacea*, $^{100}/_{1}$ (after Carpenter).

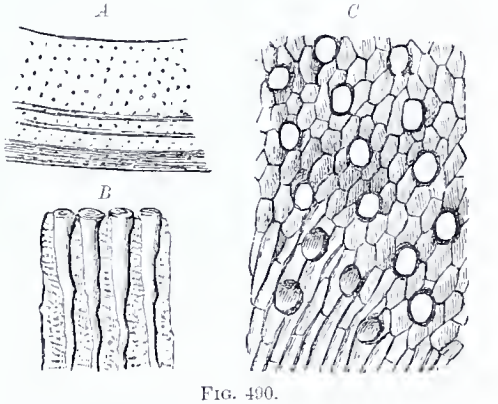


Fig. 490.

A, Punctate exterior of a Terebratuloid shell, slightly enlarged. *B*, Vertical section of shell of *Magellania flavescens*, showing distally enlarged tubules, $^{100}/_{1}$. *C*, Inner surface of *Magellania* shell showing ends of tubules and oblique calcareous prisms, $^{100}/_{1}$ (after Carpenter).

or absence of tubuli, Brachiopods are distinguished as *punctate* or *impunctate*.

The *Craniidae* have thick shells composed of concentric layers of carbonate of lime. In *Crania* the shell substance is homogeneous, and punctured by distally branching canals. In the *Lingulidae* and *Obolidae* the shell consists of alternating layers of phosphate of lime, admixed with lime carbonate, and a lustrous horny substance known as *ceratin*. The calcareous layers are prismatic, and are traversed by fine tubuli (Fig. 491). It is believed that the function of the punctae is for respiration, but the fact that these extensions of the mantle are not exposed to the water may not accord with this explanation.

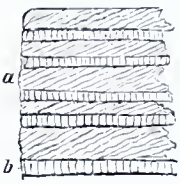


FIG. 491.

Vertical section of a *Lingula* shell, showing alternate corneous (*a*) and calcareous (*b*) layers. Strongly magnified (after Gratiolet).

Valves.—Brachiopods are delicately constituted animals, covered by two very vascular mantle lobes which secrete the calcareous or corneo-calcareous valves, of which one is *dorsal* and the other *ventral* in position. The valves are often thin and of unequal size, but the inequality is never of such a nature as to disturb the bilateral symmetry of the shell.

During life the ventral valve, which is commonly the larger of the two, occupies an inferior position, and the dorsal a superior. But in describing the shell, it is always so oriented that the posterior margin, or *hinge-line*, is placed above, and the anterior one below. A line drawn from the beak to the anterior margin describes the *length*; and one at right angles to the same, in the direction of right and left, the *width*; a third line drawn perpendicularly to the other two, and passing through the centres of the valves, measures the *thickness*. In the *Protremata* and *Telotremata* the ventral valve is convex, and curved in such manner at the posterior margin as to form a *beak*. The beak may be pointed, or it may be perforated by a round opening, or *foramen*, for the protrusion of the pedicle. In many cases, however, the pedicle opening lies underneath the apex of the beak, and sometimes encroaches upon a portion of the dorsal valve. In the *Atremata* the pedicle emerges from between the two valves; in the *Neotremata* the posterior margin of the ventral valve is notched, or there may be a small, circular, eccentric perforation, or a more or less long, narrow slit. In the *Telotremata* the pedicle opening, or *delthyrium*, which is originally triangular in form, becomes either wholly or partially closed by the growth of *deltidial plates*. In the *Protremata* and certain of the *Neotremata*, the delthyrium is closed by a true *deltidium*, as this covering is called.

FIG. 492.

Cyrtina heteroclyta, Defr. sp. Ventral valve with high area and pseudodeltidium.

The *cardinal area* is a term applied to the flattened or curved triangular area which is frequently observable between the hinge-line and the beak (Fig. 492). It is more highly developed in the ventral than in the dorsal valve, and is bisected medially by the triangular *delthyrium*. A true cardinal area is absent in the *Atremata* and *Neotremata*; but when a small area is present in these orders, it is called a *false cardinal area* (Fig. 506, *B*, *C*). A split tubular structure, or *syrinx*, which partially enclosed the pedicle, is developed in the delthyrium of some spire-bearing forms.

The *deltidium* has its origin in the Cephalula stage (*Thecidea Mediterranea*) contemporaneously with the rudiments of the dorsal and ventral valves, while the embryo is still in the free, swimming condition. The dorsal valve and incipient

deltidium appear first, being secreted by the rudimentary dorsal mantle and the dorsal surface of the body, the latter subsequently becoming the pedicle. The ventral valve is formed last, but is widely separated from the dorsal. Between the two valves is placed the short and thick, but as yet unattached pedicle, on the dorsal surface of which the third plate, known as the *prodeltidium*, still remains. Shortly before the animal becomes fixed by the pedicle, the prodeltidium fuses with the posterior margin of the ventral valve. The pedicle is at this stage entirely surrounded by shell, being enclosed on one side by the ventral valve, and on the other by the deltidium. The latter plate then continues to grow as one piece, extending from the apex in an anterior direction, and is secreted entirely by the pedicle (Fig. 504). The deltidium is never punctate in structure, but it may bear spines (*Aulosteges*), and sometimes exhibits a round or pedicle perforation (*Clitambonites*). The deltidium is characteristic of the *Protremata*, but it is also developed in some of the *Neotremata* (*Acrotretacea*). This covering of the delthyrium is always present in the young of the *Protremata*, but is absent in the *Telotremata*. In many of the *Protremata* (*Orthidae*, etc.), the deltidium is only present in nepionic stages of the individual, being resorbed at maturity; but in the great majority of these forms it remains persistent throughout life. In numerous *Telotremata*, the deltidial plates unite medially at maturity, when they may resemble a true deltidium.

Deltidial plates occur only in the order *Telotremata*, and consist of two pieces, which begin as narrow, linear, calcareous plates, growing medially from the walls of the delthyrium. They gradually increase in size, and usually come in contact medially with one another, either below or above the pedicle foramen, and are secreted by an extension of the ventral mantle lobe. In this respect they differ from the deltidium of the *Protremata*, which is secreted by the pedicle. The deltidial plates are never present in the earliest growth stages of the shell, the delthyrium being then an open triangular fissure through which the pedicle is protruded. In the adult stage the deltidial plates may remain as narrow, linear, discrete plates (Fig. 493, *B*); may meet beneath the pedicle foramen (Fig. 498); or they may wholly enclose the pedicle (Fig. 493, *A*). The deltidial plates frequently unite, when they closely resemble a true deltidium (*Cyrtia*, *Cyrtina*, Fig. 492); they are then termed a *pseudodeltidium*.

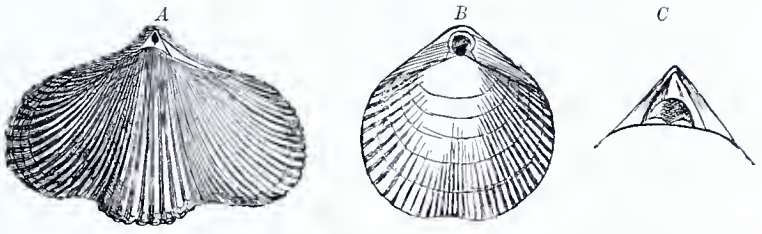


FIG. 493.

A, *Rhynchonella vespertilio*, with united deltidial plates. *B*, *Terebratella dorsata*, with discrete deltidial plates. *C*, Young specimen of *Stringocephalus Burtoni*, with the deltidial plates united above the foramen.

The *chilidium* is a convex plate which often covers the cardinal process of the dorsal valve in the *Protremata*. It is particularly well developed in the families *Clitambonitidae* and *Strophomenidae* (Fig. 538, *B*). The chilidium is not to be homologised with the deltidium, since it never appears earlier than the adolescent stage, and is apparently a secretion of the dorsal mantle lobe. Both its origin and phyletic significance are therefore very different from those of the deltidium.

The *listrium* is a plate closing the progressive track of the pedicle opening or pedicle cleft, in some *Neotremata*, posterior to the apex of the ventral valve.

Internal Characters of the Shell: *Articulation.*—The two valves are held in apposition either by muscles only (*Atremata* and *Neotremata*), or they are united by articulation (*Protremata* and *Telotremata*). In the latter case there are to be seen in the ventral valve a pair of cuneate or tooth-shaped

projections, one on either side of the delthyrium, called the *hinge-teeth* (Fig. 498, *B*), which fit into the so-called *dental sockets* of the dorsal valve. Articulation is also aided by the *cardinal process*, which is a more or less well-developed apophysis of the dorsal valve, and is received between the teeth of the ventral valve. By the contraction of the muscles attached to the cardinal process, the valves are opened along the anterior and lateral margins; but when shut, the test entirely encloses the soft parts of the animal.

The dental sockets are bounded on the inside by *hinge-plates* (Fig. 498, *A*), which are often supported by vertical or inclined *septal plates* extending to the bottom of the shell. The teeth of the ventral valve are sometimes supported by lamellae known as the *dental plates*. In addition to the dental plates, which frequently attain considerable size, there may be a *median*

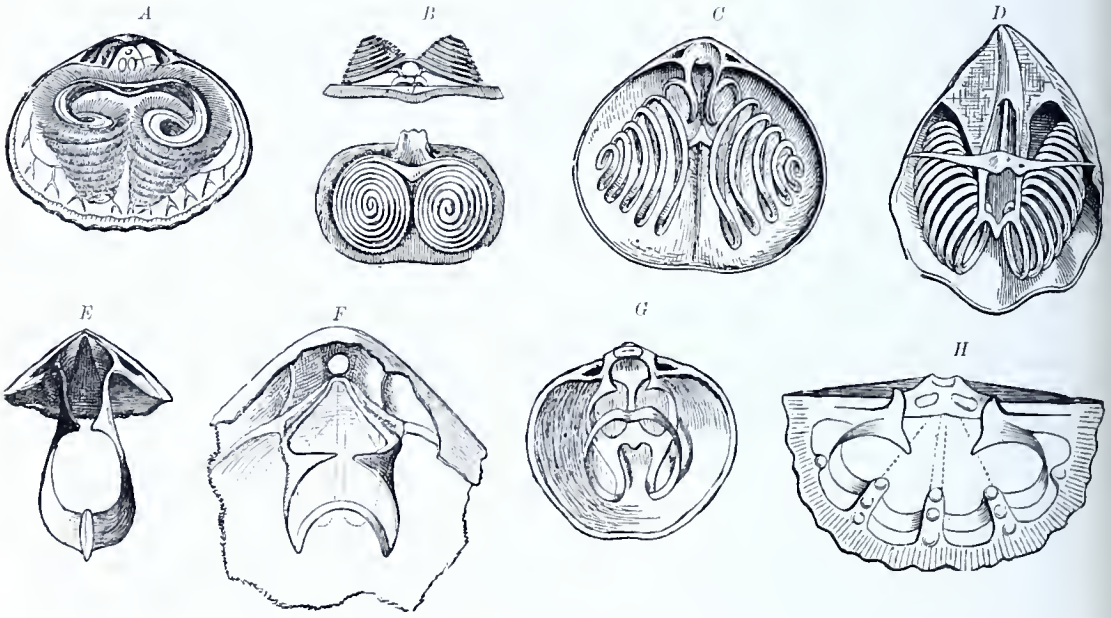


FIG. 494.

Different forms of brachidia. *A*, *Rhynchonella*; fleshy arms supported by two simply curved crura. *B*, *Thecospira*; inwardly coiled double spires, or spiralia. *C*, *Nucleospira*; and *D*, *Cyrtina*; outwardly coiled spiralia. *E-H*, Loops of Brachiopods. *E*, *Centronella*; *F*, *Diclasma*; *G*, *Terebratella*; *H*, *Megathyris*.

septum of variable proportions. This may begin beneath the beak of the valve, and may sometimes extend as far as the anterior margin (Fig. 498, *A*). Some forms are also provided with lateral septa (*Thecidiidae*).

Brachial supports.—Of special systematic importance are the *brachidia*, or internal skeleton of the fleshy arms (Fig. 494), which occur in the *Spiriferacea* and *Terebratulacea*. The brachidia are, as a rule, united basally with the *crura*, and are extremely variable in form. They usually pass through a more or less complex series of metamorphoses during the growth of the individual, and do not attain their complete development until the animal has reached maturity.

The simplest form of brachial supports is found in the *Rhynchonellacea* and *Pentameracea*, where it consists of two short, or only moderately long, curved processes called the *crura* when discrete, and *cruralium* when the plates are united. The crura are attached to the hinge-plates. The cruralium is

formed by the union of the crural plates in the *Pentameracea*. It serves for the attachment of muscles, and may either rest upon the bottom of the valve, or may be supported by a median septum. When the crura remain separate, and are therefore not for muscular insertion, they are homologous with and the equivalent of the crura in the *Rhynchonellidae*.

In the *Spiriferacea*, two thin, spirally coiled ribbons, or *spiralia*, are attached to the crura; the coils exhibiting great diversity in form, in the number of volutions, and in the direction of the hollow cones (Fig. 494, *B*, *C*, *D*). The spiralia are usually joined by a transverse band or *jugum* (Fig. 494, *D*). When the latter is discontinuous, the parts are called the *jugal processes*. The bifurcations of the jugum may enter between the convolutions of the spiralia, and may be continuous with them to their outer ends, forming what is termed a double spiral or *diplospire* (Fig. 494, *B*). In the *Terebratulidae*, the brachia are also attached to the crura, and form free, shorter, or longer *loops*, which depend toward the anterior margin (Fig. 494, *E*, *F*, *G*). The two *descending branches* may either unite directly or may be joined by a *transverse band;* or the descending branches may recurve, continue upward as *ascending branches*, and be connected posteriorly by a transverse band. In the *Terebratellidae*, during all or some portion of the animal's existence, the loops are attached to a median septum by outgrowths from the descending lamellae. In the *Stringocephalidae* and *Megathyrinae* (Fig. 494, *H*), the descending branches are parallel to the lateral margins of the shell, and unite along the median line; but in some degenerate species, the loop is represented by a transverse band situated centrally on the median septum. The entire form of the brachidia is manifestly dependent upon the character of the convolutions of the fleshy arms. In recent *Rhynchonellae* (Fig. 494, *A*) the brachia form hollow spiral cones, and if we imagine these as supported by a calcareous framework, the result will be the form of support seen in the *Atrypidae*. The fleshy arms of the *Terebratellidae* are continuous with, and have at first the form of the loop, but later develop a coiled median arm. Here the loops only have calcareous supports; but in the *Spiriferacea*, the entire brachia are provided with an internal calcareous skeleton.

The changes in the form of the brachidia in the *Telotremata* during the ontogenetic stages of the individual furnish very important data in regard to the relationships existing between the different groups. In the *Spiriferacea*, not only do the number of convolutions of the spirals increase with age, but the brachidia begin with *Centronella*- and *Dielasma*-like loops, from the outer ends of which the spires are developed. Still more striking are the metamorphoses which the loops of the *Terebratulacea* undergo. According to Oehlert and Beecher, the loop of the living austral genus *Magellania* passes through stages which correspond successively to those of *Gwynia*, *Cistella*, *Bouchardia*, *Magas*, *Magasella*, *Terebratella*, and *Magellania;* and Fricle has shown that the metamorphoses of the loop in the boreal form *Macandrevia cranium* correspond in succession to the genera *Platidia*, *Ismenia*, *Mühlfeldtia*, *Terebratalia*, and *Macandrevia*.

A knowledge of the character of the brachidia in the *Spiriferacea* and *Terebratulacea* is almost always requisite for critical generic determinations. But an examination of the interior of the shell in fossil Brachiopods often involves great difficulties, owing to the infiltration of calcite, or the filling up

of the shell cavity with sediment. Not infrequently the shell and the brachidia are secondarily replaced by quartz; and if the interior filling matter be dissolved away by dilute hydrochloric acid, exquisite preparations may be obtained, often revealing the minutest details. Sometimes hollow shells are found, in which the brachidia are well preserved; but these structures generally are more or less encrusted. It is often necessary to remove the ventral valve, when the infiltrated material can be cut away by the use of proper tools. Success in manipulations of this kind requires not only considerable dexterity, but the conditions of preservation must have been very favourable. The brachidia must be perfectly preserved, and the surrounding matrix must admit of being removed without injury to the specimen. When other expedients fail, recourse can still be had to polishing, the shell being gradually ground down by abrasion with emery powder on a glass plate. The beaks are first ground away, until the first traces of the crura appear; the surface is then cleaned and kept moistened while a careful drawing is made. Grinding is resumed for a short interval, when the surface is again cleansed and drawn. This process is repeated until the sections include the entire brachial support. From the series of transverse sections thus obtained, the brachidium can be ideally reconstructed.

The *spondylium* is an internal ventral plate traversing the posterior portion of the valve (Fig. 538, *C*). On the superior surface of the plate are inserted the adductors, diductors, and the ventral pedicle muscles. Beneath the spondylium, which may be supported by a median septum, are situated the reproductive organs. The plate is homologous with the solid or excavated *platform* of the *Atremata* (*Trimerellidae* and *Lingulasmatidae*).

The Animal: *Mantle*.—Lining the entire inner surface of the shell is a thin, transparent membrane, which appears in the embryonic condition as two distinct lobes of the thoracic segment in the Cephalula stage. This is the mantle or *pallium*, which is primarily concerned in the secretion of the shell. In *Crania* it consists of three layers: a middle cartilaginous, an inner ciliated one, and an outer layer of cells. The layer lying against the surface of the shell is often studded with minute *caeca* or blind tubes, which enter the perforations of the test. The mantle (or certain of its layers) is folded upon itself at various points, enclosing cavities or *pallial sinuses*, which contain the circulating fluids, and frequently portions of the *genital organs*. Distinct impressions of these sinuses are often observable in the valves of both recent and fossil specimens (Fig. 495). In all the greater sinuses of the mantle, in the perivisceral cavity, and in the cavernous brachia and cirri, occur calcareous *spicules* of various shapes. These are especially abundant in the *Thecidiidae*, and form an irregular mass or network. They appear to be absent in *Magellania*, *Terebratella*, and *Lingula*. The outer margins of the mantle are thickened and set with numerous, chitinous, simple, or barbed *setae*, sometimes of great length.

Fig. 495.

Camarophoria Humbletonensis, Howse. Permian; Humbleton, England. Cast showing impressions of pallial sinuses (after Davidson).

The shell cavity is divided by a vertical membranous wall, which is an extension of the mantle, into two regions: a posterior, or *visceral cavity*,

and an anterior, or *brachial cavity*. The posterior cavity contains the principal viscera, the alimentary, circulatory, nervous, and muscular systems. The anterior chamber is occupied by the arms.

Organs of the visceral cavity.—The membranous partition is pierced centrally by the oval or slit-like *mouth*, from which the *digestive tube* extends backwards as a simple or bent canal. In inarticulate species, the alimentary canal is very long, makes several convolutions, and terminates in a well-defined *anus*, situated on one side of the animal. In the *Protremata* and *Telotremata*, the digestive tube is shorter and much simpler than in the *Atremata* and *Neotremata*. The intestine makes a single convolution and terminates blindly in the living representatives of these orders, being surrounded by large hepatic lobes. In many Palaeozoic species it probably did not terminate blindly, since the intestine passed through the hinge-plate by a central foramen. There is no heart, circulation being apparently maintained by the cilia lining the vascular sinuses. These sinuses pass into the perivisceral chambers, and are developed into vascular dilations at the back of the stomach and elsewhere. These bodies are not contractile, and their function is unknown. Two numerously branched *vascular trunks* diverge from the anterior portion of the perivisceral chambers, traversing the mantle in either valve to its margins, and several others pass over the fleshy brachia for their entire length. The *nervous system* consists of a circum-oesophageal ring on which two supra-oesophageal ganglia are inserted. From the swellings of the oesophageal ring (notably from that on the lower side), nerve fibres are given off to the brachia, muscles, pedicle, and the two lobes of the mantle. In adult Brachiopods, *sense organs* are not known with certainty; but in the embryos such are believed to be present. So far as is known the sexes are always separate. The *sexual organs* in both male and female are located essentially alike, and have a paired arrangement. Generally they occupy the main trunks of the vascular sinuses, but may extend into the visceral chamber, or in some of the inarticulate forms, may be restricted to the latter.

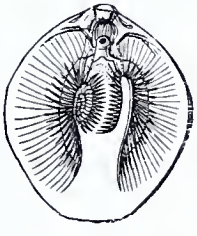


Fig. 496.

Liothyrina vitrea, Linn. sp. Recent. Fleshy brachia simply recurved.

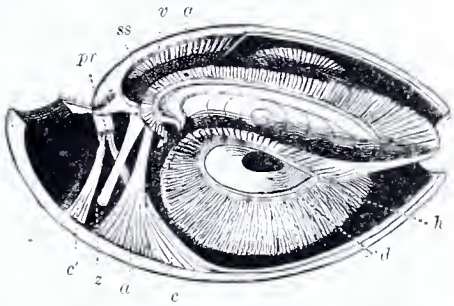


Fig. 497.

Magellania flavescens, Val. Median vertical section, slightly enlarged. *d*, Spiral brachia; *h*, Fringed brachial margin; *pr*, Cardinal process; *z*, Alimentary canal; *v*, Mouth; *ss*, Septum; *a*, Adductors; *c*, *c'*, Diductors (after Davidson).

The brachial cavity.—The greater part of the anterior, or brachial cavity is occupied by the spirally enrolled labial appendages, the so-called *arms*, or *brachia*. These are two in number, one at each side of the mouth, and are of extremely delicate constitution (Figs. 496, 497, and 494, *A*). The tissue of which they are composed is essentially cartilaginous, and is traversed by several circulatory canals as well as by a groove. The outer edges of the brachia are fringed with long and movable *cirri* or *tentacles*, by means of which currents are set up that conduct small food particles to the mouth. The arms are frequently supported by a slender calcareous framework called

the brachial supports, or *brachidia*, described above. There are no special respiratory organs, the blood being oxygenated in the inner surface of the mantle and in the spiral arms, where it is brought into close osmotic relation with the water.

Muscular system.—By means of muscles Brachiopods are enabled to open and close their valves, and to a limited extent can protrude and retract the pedicle. In the articulate forms (*Protremata* and *Telotremata*) there are three sets of muscles—namely, the *diductors*, which by contraction open the valves; the *adductors*, which by contraction close the valves; and the *pedicle muscles*, or *adjustors*, which also by contraction withdraw the pedicle. The points of attachment of these muscles leave more or less distinct impressions in the valves of both recent and fossil Brachiopoda, and the subject is therefore worthy of careful examination.

The *adductor*, or closing muscles are attached on either side of the median line in the dorsal valve, and leave two elongate scars lying immediately to the right and left of the median line, enclosed between the diductors (Fig. 498, *B*, *a*). These muscles extend almost directly from one valve to the other, and as each muscular band is once divided, their insertions on the dorsal valve are quadruple. Their impressions on this valve are known as the anterior and posterior adductors (Figs. 498, *A*, *B*, *a*, *a'*).

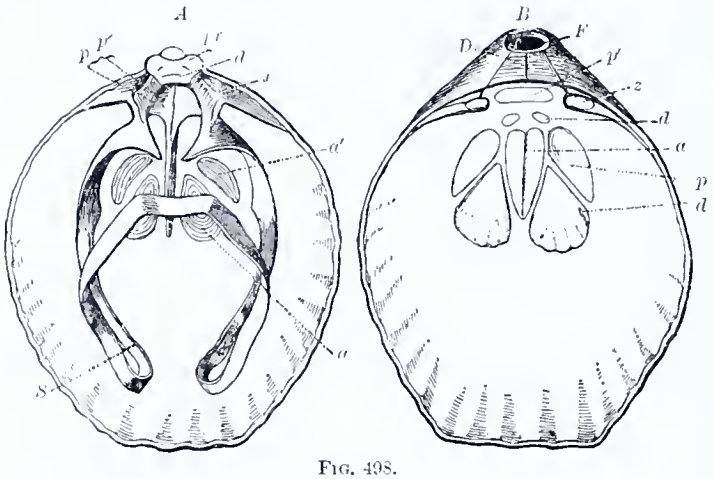


Fig. 498.

Magellania flavescens, Val. Recent; Australia (after Davidson). *A*, Dorsal valve. *B*, Ventral valve. *D*, Deltidial plates. *F*, Foramen. *S*, Loop. *pr*, Cardinal process; *x*, Hinge-plate; *z*, Hinge-teeth; *a*, *a'*, Impressions of adductors; *d*, *d'*, Diductors: *p*, *p'*, Pedicle muscles.

The principal *diductors*, or opening muscles, originate at the anterior ventral edge of the visceral area, and on either side of the median line; the scars of these muscles being usually the largest and deepest of any in the animal. They taper rapidly in crossing the interior cavity, and their small extremities are attached to the anterior portion of the cardinal process. There are also inserted on the cardinal process, behind the principal diductors, two much smaller muscular bands, which are called the *accessory diductors*. Their attachment on the ventral valve is represented by two feeble scars in the posterior part of the muscular region, but these are rarely observable in fossil specimens (Fig. 498, *A*, *B*, *d*).

When a functional pedicle is present, there are found in addition to the valvular muscles two pairs (one to each valve), and a single unpaired muscle; these are attached to the pedicle, and are called the *pedicle muscles* (Fig. 498, *B*, *p*, *p'*). The pair in the ventral valve originates immediately outside of and posterior to the adductors and diductors; the pair in the dorsal valve is attached behind the posterior adductors; and the unpaired muscle lies at the base of the pedicle in the ventral valve. Only the latter unpaired band, as a rule, leaves a perceptible scar in fossil specimens.

The entire muscular system in the *Protremata* and *Telotremata* works with the utmost precision. The cardinal process is received between the teeth of the ventral valve in such a manner as to allow the dorsal valve to swing freely in the median

vertical plane as on hinges, and at the same time prevents motion in a lateral direction. The diductors, being attached to the cardinal process, act upon a lever arm when they contract, thus opening the valves, while the contraction of the adductors serves to close them (Fig. 497).

In the *Atremata* and *Neotremata* the muscles are arranged differently, and are often more complicated and numerous, as articulation is usually not present in these orders. The greatest complexity is attained in *Lingula* (Fig. 499), because these animals, in addition to the absence of articulation, slide their valves laterally.

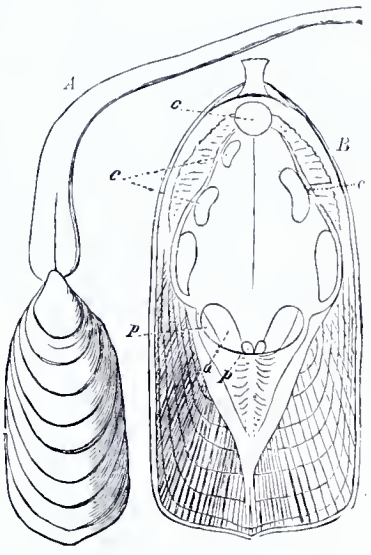


Fig. 499.

Lingula anatina, Brug. Recent. *A*, Shell with pedicle, natural size *B*, Interior of ventral valve showing muscular impressions; *a*, Adductors; *c*, Protractors; *p*, Retractors; *o*, Pedicle muscle.

Ontogeny.—The development of Brachiopods from the egg to maturity may be divided into two periods: (*a*) stages of growth from the egg to that condition in which the animal is recognisable as possessing some distinctive class characters; and (*b*) from the first shelled condition, or protegulum, to maturity and old age.

Our knowledge of the earliest embryonic conditions is restricted to *Terebratulina*, *Liothyrina*, *Cistella*, and *Thecidea*. After fertilisation the larvae may remain attached, and pass their early stages within the parent; or they may develop cilia before segmentation, and be set free in the pallial chamber or in the sea-water. The free larvae swim by the aid of cilia with a twirling motion. There are five well-marked stages of growth before the larvae can be definitely recognised as Brachiopods. These are: (1) The *Protembryo*, which includes the ovum, its segmented stages preceding the formation of a blastula, or primary internal cavity (Fig. 500, *A*, *B*); (2) the *Mesembryo*, or blastosphere, a multi-segmented larva with an internal cavity (Fig. 500, *C*); (3) the *Metembryo*, or gastrula stage (Fig. 500, *D*); (4) the *Neoembryo*, or segmented ciliated

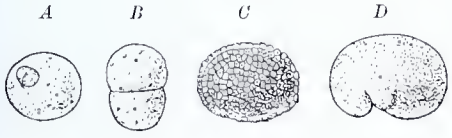


Fig. 500.

Cistella Neapolitana, Schacchi. Recent. *A*, Protembryo; unsegmented ovum. *B*, Protembryo; ovum composed of two spheres. *C*, Mesembryo; blastosphere. *D*, Metembryo; Gastrula (after Shipley, from Beecher).

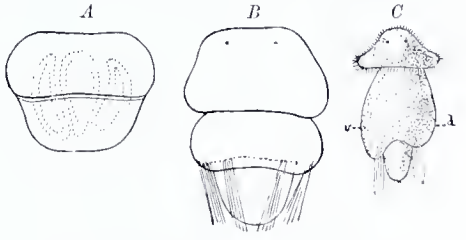


Fig. 501.

Cistella Neapolitana, Schacchi. *A*, Neoembryo; embryo of two segments. *B*, Neoembryo; cephalula, ventral side, showing cephalic, thoracic, and caudal segments, eye-spots, and bundles of setae. *C*, Neoembryo; lateral view of completed cephalula stage, showing extent of dorsal (*d*) and ventral (*c*) mantle lobes, and umbrella-like cephalic segment. (*A* and *B* after Kovalevski, *C* after Shipley; all reproduced from drawings by Beecher.)

Cephalula, which consists at first of a cephalic lobe, bearing eyes in *Cistella*, and a caudal lobe, to which is added later a thoracic segment carrying four bundles of setae. At the same time the dorsal and ventral sides of the latter segment become extended over the caudal lobe, and are progressively defined as two lobes (Fig. 501); (5) the *Typembryo*, or larval stage, in which the dorsal and ventral thoracic lobes, or mantle, fold over and enclose the cephalic lobe (Fig. 502, *B*). Upon the mantle lobes, either before or after turning, there is a corneous integument which develops into the protegulum before the formation of the true shell. The caudal segment

becomes the pedicle, and may in this stage serve to attach the larvae to foreign objects, or the pedicle may remain undeveloped for a time. A rudimentary digestive tract is present, and also four pairs of muscles, which later become the adductor, diductor, and ventral pedicle muscles.

In the *Phylembryo* the *embryonic* shell, or *protegulum*, is completed; the tentacular lobes of the lophophore, or brachia, appear; the four bundles of setae are dehisced; obsolescence of the eyes occurs, as well as the agreement of the muscular system with that in adult forms.

The *protegulum* has been observed by Beecher in many genera, representing nearly all the leading families of the class, and therefore it may be inferred that the protegulum is common to all Brachiopods. It is semi-circular or semi-elliptical in outline, with a straight or arcuate hinge-line, and no cardinal area. The prototype preserving throughout its development the main features of the protegulum, and showing no separate or distinct stages of growth, is represented by the genus *Paterina* (Fig. 505).

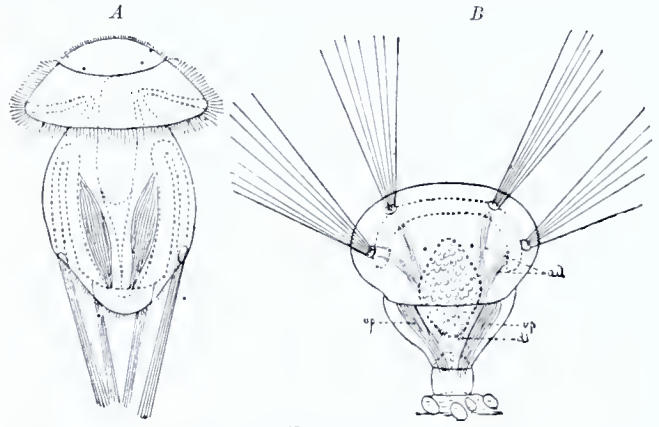


Fig. 502.

Cistella Neapolitana, Schacchi. *A*, Neoembryo; completed cephalula stage. *B*, Typembryo; transformed larva resulting from folding upwards of mantle lobes over cephalic segment; *ad*, Muscles from bundles of setae to sides of body cavity; *di*, Muscles from dorsal to ventral sides of body; *vp*, Muscles from ventral side of body to caudal segment or pedicle (after Kovalevski, from Beecher).

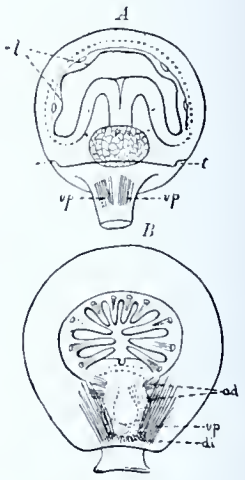


Fig. 503.

Cistella Neapolitana, Schacchi. *A*, Phylembryo; Brachiopod showing shell (protegulum), beginning of tentacles of lophophore (*l*), obsolescence of eye-spots, and formation of oesophagus; *t*, Hinge-teeth; *vp*, Ventral pedicle muscles. *B*, Nepionic Brachiopod, showing distinct tentacles of lophophore, mouth and stomach, and transformation of muscles from typembryo; *ad*, Adductors; *di*, Divaricators; *vp*, Ventral pedicle muscles (after Kovalevski, from Beecher).

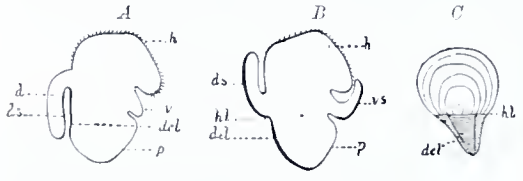


Fig. 504.

Thecidia (*Lacazella*) *Mediterranea*, Risso. Recent. *A*, Dorso-ventral longitudinal section of cephalula; *h*, Head; *d*, Dorsal mantle lobe; *v*, Ventral mantle lobe; *ds*, Beginning of dorsal valve; *del*, Shell plate forming on dorsal side of body; *p*, Pedicle. *B*, Dorso-ventral longitudinal section of typembryo; *vs*, Ventral valve; *hl*, Hinge-line of dorsal valve. *C*, Adult specimen seen from the dorsal side, showing ventral area and deltidium. (*A* and *B* after Kovalevski; *C* after Beecher.)

So far as observed, the protegulum, or *Paterina stage*, in the *Atremata* and *Telotremata* is followed by the *Obolella stage* of nearly circular outline. After this stage, specific characters appear, and in the open delthyrium of the *Telotremata* there are usually developed the first rudiments of the deltidial plates. In the *Protremata*, the Paterina stage is not followed by the Obolella stage, but the wide delthyrium of the protegulum is at once affected and modified by the prodeltidium, which develops into the deltidium. In the *Acrotretacea*, belonging to the *Neotremata*, there is often developed a true deltidium, showing the close relationship of the order with the *Protremata*, and the dissimilarity of these two orders to *Atremata* and *Telotremata*. In the *Discinacea*, belonging to the *Neotremata*, the pedicle opening is an open notch in the posterior

margin of the ventral valve. In derived forms this is progressively closed posteriorly ; geologically in the phylum, and ontogenetically in the latest derived individuals.

Habitat and Distribution.—Brachiopods are usually gregarious in habit, often growing in clusters attached to one another. This is not only true of recent species, but of Palaeozoic forms as well. Brachiopods are found in all latitudes and at all depths, occurring most abundantly between tides and 278 fathoms. *Liothyrina Wyvillii* was dredged from the enormous depth of 2945 fathoms. *Terebratulina caput-serpentis* ranges from a few fathoms to a depth of 1195 fathoms.

Brachiopods are most prolific in warmer seas, the Japanese province having nearly thirty species. As a rule, those occurring in cold waters are not found in warm waters. Oehlert has shown, however, that a few species are world-wide in their distribution (*Liothyrina vitrea*, var. *minor* and *Terebratulina caput-serpentis*), and that they also have great bathymetric range. Some generally distributed Palaeozoic species are *Atrypa reticularis*, *Leptaena rhomboidalis*, and *Productus semireticulatus*.

Migration of Brachiopods is possible only during the early larval stages, and then to a very limited extent. Morse observed that *Terebratulina* became attached in a few days, but Müller kept *Discinisca* in confinement nearly a month before any became sessile. Deep-sea Brachiopods are usually thin-shelled, brittle, and translucent.

Colour.—"The shells of most living species are of light or neutral tints, white or horn-colour. A deep orange-red in radiating bands or in solid tints, colours some species (*Terebratulina*, *Kraussina*, etc.) ; light yellows, deep and light shades of green (*Lingula*), black in bands (*Crania*), or masses (*Rhynchonella*) embellish these shells. Even among the fossil species traces of faded colour-marks are occasionally observed ; Deslongchamps has described them among Jurassic species, Davidson among the Carboniferous, and Kayser has found a colour-marked *Rhynchonella* in the Devonian. The large highly ornamented species of Palaeozoic times, with their external sculpture heightened by a brilliant colouring, must have been objects of exquisite beauty" (Hall and Clarke).

Classification.—The Brachiopoda, since 1858, have been divided by nearly all systematists into two orders, based on the presence or absence of articulating processes. These divisions, "Articulés and Libres," were recognised by Deshayes as early as 1835, but not until twenty-three years later were the names *Lyopomata* and *Arthropomata* given them by Owen. These terms have been generally adopted by writers, though some prefer *Inarticulata* and *Articulata*, Huxley, or Bronn's *Ecardines* and *Testicardines*. Bronn (1862) and King (1873), while retaining these divisions, considered the presence or absence of an anal opening more important than articulating processes, and accordingly proposed the terms *Pleuropygia* and *Apygia*, and *Tretenterata* and *Clistenterata* respectively. In many Palaeozoic rostrate genera of *Clistenterata*, it has been shown that an anal opening was also present, and therefore the absence or presence of this organ is not of ordinal value.

The first attempt to construct a classification of the Brachiopods was that of Leopold von Buch, who took for his principal differential characters the conformation of the umbonal region, the presence or absence of a pedicle, the nature of the deltidium, and the external form and ornamentation of the shell.

While his classification lacks a perfect understanding of the features in question, it is remarkable that von Buch, nearly sixty years ago, and Deslongchamps, twenty-eight years later, recognised some of the principles upon which the classification of the Brachiopoda is now established, viz. the nature of the pedicle opening.

Up to 1846 the general external characters of the Brachiopods served the majority of authors as the essential basis for generic differentiation. In that year, however, King pointed out that more fundamental and constant characters exist in the interior of the shell, a fact which soon came to be generally recognised, mainly through the voluminous and admirable contributions of Thomas Davidson.

Waagen in 1883 found it "absolutely necessary" to divide Owen's two orders into seven sub-orders. The basis for these sub-orders rests on no underlying principle of general application, and yet five of these divisions are of permanent value, for each contains an assemblage of characters not common to the others.

No classification can be natural and permanent unless based on the history of the class (*chronogenesis*) and the *ontogeny* of the individual. However, as long as the structure of the early Palaeozoic genera remained practically unknown, and the ontogeny wholly unrevealed, nothing of a permanent nature could be attempted. In the recent and very excellent volumes by Hall and Clarke (*Palaeontology of New York*, vol. viii.), the great majority of the Palaeozoic genera are clearly defined. The ontogenetic study of the Palaeozoic species was initiated in 1891 by Beecher and Clarke, followed by Beecher, and more recently by Schuchert; and their results combined with those derived from the study of the development of some living species, such as have been published by Kovalevski, Morse, Shipley, Brooks, Oehlert, Beecher, and others, confirm the conclusion reached through chronogenesis. Moreover, the application by Beecher of the law of morphogenesis, as defined by Hyatt, and the recognition and establishment of certain primary characters have resulted in the discovery of a fundamental structure of general application for the classification of these organisms. It has for its foundation the nature of the pedicle opening and the stages of shell growth. On this basis Beecher (1891) has divided the class into four orders: the *Atremata*, *Neotremata*, *Protremata*, and *Telotremata*.

The nature of the pedicle opening being employed for ordinal divisions, persistent internal characters of the shell are, as a rule, used for superfamily purposes. Such are the presence or absence of a spondylium, brachial supports, etc. Family divisions are based upon a combination of external and internal generic characters, such as the outer form, nature, and position of muscles, internal plates, etc.

No division, however, has any value unless the group contains forms of but one phylum, since a phylum or line of descent cannot originate twice. However, it happens that the same or nearly the same combination of mature characters is developed along different lines; and when this occurs the ontogeny will show it. It is therefore not correct to group different stocks under one and the same genus. For instance, the family *Terebratellidae* probably divided during early Mesozoic times, one stock drifting into boreal and another into austral regions. These two stocks agree structurally in the earliest shelled condition and also at maturity; but between these two stages

of growth, the austral group (*Magellaninae*) passes through a different series of loop metamorphoses from the boreal one (*Dallinae*).

It was by the application of the above-mentioned principles that Schuchert, in 1893, arranged all the genera of Brachiopoda under the four orders instituted by Beecher. Further attention has since been given to this subject by the same writer, and the classification outlined in his *Synopsis of American Fossil Brachiopoda* has been adopted in the present work.

Order 1. ATREMATA. Beecher.

Inarticulate Brachiopoda with the pedicle emerging freely between the two valves, the opening being more or less shared by both. Growth taking place mainly around the anterior and lateral margins, never enclosing or surrounding the pedicle. Aperture unmodified. Prodeltidium attached to dorsal valve.

Superfamily 1. OBOLACEA. Schuchert.

Rounded or semi-circular, and more or less lens-shaped, thick-shelled, primitive Atremata, fixed by a short pedicle throughout life to extraneous objects. Cambrian to Silurian.

Family 1. Paterinidae. Schuchert.

Obolacea with nearly semi-circular valves without cardinal areas, and with the entire, gaping, posterior region occupied by the pedicle. This is the simplest shelled condition of the class, and is repeated ontogenetically as the protegulum, or initial shell, probably throughout the class. Cambrian.

Paterina, Beecher (Fig. 505). Of this North American genus, the only one of the family, about six species are known.

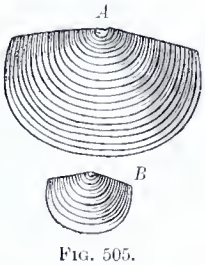


Fig. 505.

Paterina Labradorica, Bill. Cambrian; near Georgia, Vermont. *A*, Dorsal valve, 3/1. *B*, Ventral valve of young specimen, 3/1 (after Beecher).

Family 2. Obolidae. King.

Thick-shelled Obolacea, of nearly circular or ovoid outline, biconvex, usually smooth, and with rudimentary cardinal areas traversed by shallow pedicle grooves. Muscular scars distinct, consisting of two pairs of adductors and three of sliders, or adjustors. Cambrian.

Under this family are included some of the oldest known Brachiopods. The family is abundantly represented in the Lower and Middle Cambrian.

Obolella, Billings (? *Dicellomus*, Hall). Small, oval, or round shells, with narrow cardinal areas. Dorsal valve usually with a rudimentary hinge facet. North America and Europe.

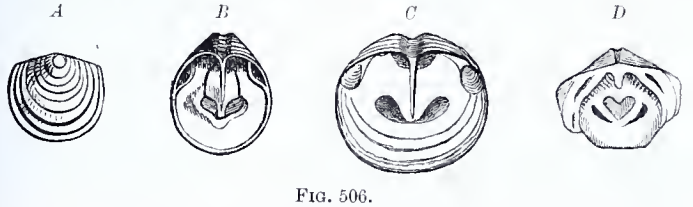


Fig. 506.

Obolus Appolinis, Eichw. Cambrian; St. Petersburg, Russia. *A*, Exterior of dorsal valve. *B*, *C*, Interior of ventral valve. *D*, Interior of dorsal valve. Natural size.

Fig. 507.

Spondylobolus craniolaris, M'Coy. Ordovician; Ireland. Natural size (after Davidson).

Elkania, Ford (*Billingsia*, Ford). Like *Obolella*, but with a small platform in the dorsal shell. North America.

Obolus, Eichwald (*Ungula*, Pander; *Ungulites*, Bronn; *Aulonotreta*, Kutorga; *Acritis*, *Schmidtia*, Volborth), (Fig. 506). Much like *Obolella* externally, but larger and with more prominent cardinal areas in both valves. Ventral valve with a median septum extending to about the centre of the valve. *O. Appolinis*, Eichwald, occurs in vast numbers in the Unguliten-Sandstein of Russia.

Neobolus, Waagen; India. *Botsfordia*, Matthew; New Brunswick. *Spondylobolus*, M'Coy (Fig. 507). Ireland.

Family 3. **Trimerellidae**. Davidson and King.

Large, thick-shelled, inequivalved Obolacea, with the ventral cardinal area usually very prominent, triangular, and tranversely striated. Adjustor and anterior adductor muscles elevated upon solid or excavated platforms. Cambrian to Silurian.

Dinobolus, Hall (*Conradia*, Hall; *Obolellina*, Billings). Cardinal area not so prominent as in the other genera of this family. Platform small, with abruptly conical vaults. Ordovician and Silurian; North America, Great Britain, Bohemia, Gottland, and Esthonia.

Monomerella, Billings. Similar to *Trimerella*, with well-developed platforms

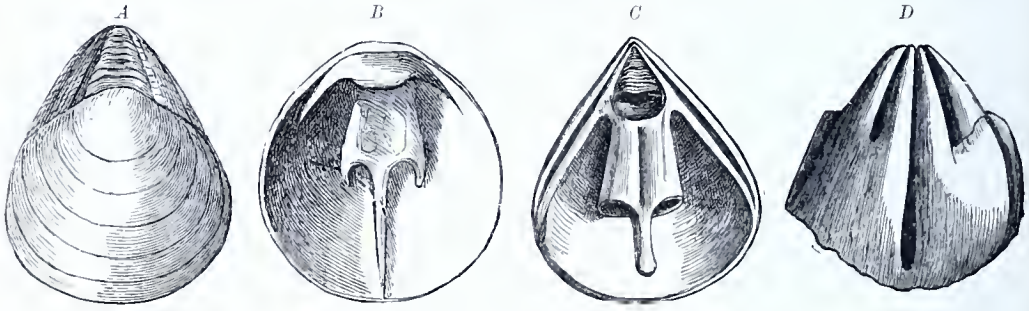


FIG. 508.

Trimerella Lindstroemi, Dall sp. Silurian; Gottland. × 1/2. *A*, Shell seen from the dorsal side. *B*, *C*, Interior of dorsal and ventral valves, respectively. *D*, Cast. (*A* and *B* after Davidson; *C* and *D* after Lindström.)

in both valves; that of the dorsal valve, however, but slightly excavated. Silurian; North America, Gottland, and Livonia.

Trimerella, Billings (*Gotlandia*, Dall), (Fig. 508). Platforms long, narrow, well-developed, and doubly vaulted. Dorsal beak often thickened into a prominent apophysis extending against the cardinal slope of the ventral valve. Silurian; North America, Gottland, and Farö.

Rhinobolus, Hall. Silurian; North America. (?) *Lahkmina*, Oehlert (*Davidsonella*, Waagen). Lower Cambrian; India.

Superfamily 2. LINGULACEA. Waagen.

Elongate, thin-shelled, burrowing, derived Atremata, with a more or less long, worm-like, tubular, flexible pedicle. Cambrian to Recent.

Family 1. **Lingulellidae**. Schuchert.

Spatulate, inequivalved Lingulacea, structurally intermediate between the Obolidae and Lingulidae. Cambrian and Ordovician.

This family contains the oldest Linguloid shells, the members of which still retain a preponderance of Oboloid characters. The first true *Lingulae* appear in the Lower Ordovician.

Lingulella, Salter. Linguloid shells with the ventral cardinal area more or less elevated beyond the dorsal shell, and bisected medially by a narrow pedicle furrow. Cambrian; North America and Europe.

This genus is not well known, and the species referred to it may belong to two or more genera. The Lower Cambrian forms have decided Obolella-like muscular scars, while those of the type species seem to be more in harmony with *Lingula*.

Lingulepis, Hall. Pedicle valve generally much produced at the beak, with no distinct cardinal area; dorsal valve more or less ovate. Cambrian; North America.

Leptobolus, Hall. Very small Linguloid shells, with well-developed, distinctly grooved, cardinal areas in both valves. Interior marked by two or three diverging, slightly elevated septa, which sometimes are somewhat bifurcated terminally. Ordovician; North America.

(?) *Paterula*, Barrande. Ordovician; Bohemia and North America.
(?) *Miekwitzia*, Schmidt. Lower Cambrian; Sweden.

Family 2. **Lingulidae**. Gray.

Attenuate, sub-quadrate, or spatulate, almost equivalved Lingulacea, with a more or less long, tubular, flexible pedicle. Muscles highly differentiated and consisting of six pairs, two of adductors, and four of sliders, or adjustors. Ordovician to Recent. Maximum development in Ordovician, declining after Devonian time.

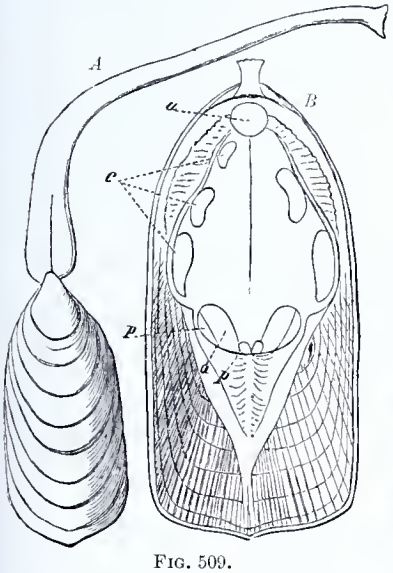


Fig. 509.

Lingula anatina, Brug. Recent. *A*, Shell with pedicle. *B*, Interior of ventral valve.

Lingula, Bruguière (s. g. *Glossina*, Phill.), (Figs. 509 and 510). Shell thin, usually compressed, glistening, generally smooth, or with fine, concentric, more rarely with both concentric and radial striae; broad over the pallial region, tapering more or less toward the beaks. Ordovician to Recent. Maximum development in Silurian and Devonian.

Fig. 510.

Lingula Lewisii, Sow. Silurian; Gottland.

Glottidia, Dall. Like the preceding, but interior of ventral valve with two septal ridges diverging from the beaks. Dorsal valve with a single median ridge. Recent; American seas.

Dignomia, Hall. Both valves with median septal ridges; that of the dorsal valve stronger, and flanked by two submarginal diverging ridges, which correspond in position to grooves in the ventral valve. Middle Devonian; North America.

Barroisella, Hall and Clarke. *Lingulae* with rudimentary articulation. Silurian to Devonian; North America; (?) Bohemia.

Thomasina, Hall and Clarke. *Lingulae* with the posterior margin of the ventral valve notched, and with two conspicuous articulating processes. Silurian; France.

Family 3. **Lingulasmatidae.** Winchell and Schuchert.

Platform-bearing Lingulacea derived through Lingulidae. Ordovician and Silurian.

Lingulops, Hall. Small *Lingulae* with narrow, depressed, not excavated, platforms. Ordovician and Silurian; North and South America.

Lingulasma, Ulrich. Large thick-shelled *Lingulae* with very prominent, slightly excavated platforms. Ordovician; North America; (?) England.

Order 2. NEOTREMATA. Beecher.

Circular or oval, more or less cone-shaped, inarticulate Brachiopoda, with the pedicle opening restricted throughout life to the ventral valve. Pedicle aperture modified by a deltidium or listrium. Prodeltidium attached to the ventral valve.

Superfamily 1. ACROTRETACEA. Schuchert.

Neotremata with phosphatic shells and a more or less well-developed deltidium. Dorsal protegulum marginal. Cambrian to Silurian.

Family 1. **Acrotretidae.** Schuchert.

Acrotretacea with the pedicle opening posterior to the protegulum. Cambrian to Silurian.

Acrotreta, Kutorga. Ventral valve sub-conical; the posterior margin flattened, triangular in form, and resembling a true cardinal area. This slope is divided medially by a shallow groove, widening downward. Circular pedicle opening at the apex of the valve. Dorsal valve flat or depressed, convex; interior flanked by a large anterior and a smaller posterior pair of muscular impressions; exterior concentrically striated. Cambrian and Ordovician; North America and Europe.

Conotreta, Walcott. Small, highly conical shells, with the interior of the ventral valve marked by a number of radiating ridges. Ordovician and Silurian; North America.

Acrothele, Linnarsson. Rounded, or broadly oval, depressed shells with the cardinal area obsolete. Cambrian; North America and Europe.

Linnarssonia, Walcott. Smaller and more conical shells than *Acrothele*. Cambrian; North America and Europe.

Discinopsis, Matthew; New Brunswick. *Iphidea*, Billings; North America and Sweden. *Volborthia*, von Möller; Russia. (?) *Mesotreta*, Kutorga; Russia. (?) *Orbicella*, d'Orbigny (*Keyserlingia*, Pander). (?) *Helmersenia*, Pander; Russia. All Cambrian.

Family 2. **Siphonotretidae.** Kutorga.

Acrotretacea with the pedicle opening passing by resorption anteriorly through the protegulum and the umbo of the shell. Cambrian to Silurian.

Siphonotreta, de Vern (Fig. 511). Shell elongate-oval, moderately convex. Pediele opening at the apex, and communicating with the interior of the shell by a tubular canal. Cardinal area and deltidium not developed. Shell ornamented with concentric lines and ridges; the epidermal layer bearing hollow spines, though rarely preserved. Layers beneath the epidermis punctured by radiating and branching tubules. Ordovician and Silurian; Europe and (?) North America.

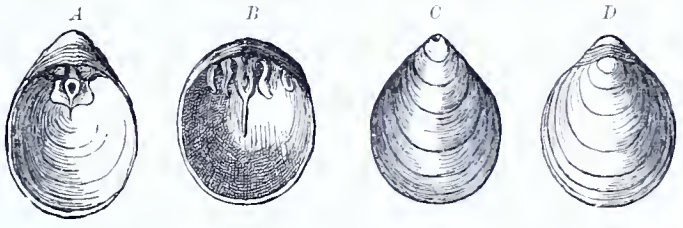


Fig. 511.

Siphonotreta unguiculata, Eichw. Ordovician; St. Petersburg. 1/1. *A*, *B*, Interior of ventral and dorsal valves, respectively. *C*, *D*, Worn exterior of shell; ventral and dorsal aspects.

Schizambon, Walcott (*Schizambonia*, Oehlert). Small depressed *Siphonotretae* without tubular pedicle canal. Ordovician; America and Russia.

Trematobolus, Matthew. *Siphonotretae* with rudimentary articulation. Middle Cambrian; New Brunswick.

Superfamily 2. DISCINACEA. Waagen.

Neotremata with phosphatic shells, a listrium, but no deltidium. Dorsal protegulum usually sub-central. Cambrian to Recent.

Family 1. Trematidae. Schuchert.

Primitive Discinacea, in which the posterior margin of the ventral valve has a triangular pedicle notch throughout life. A listrium usually present. Cambrian to Carboniferous.

Discinolepis, Waagen. Small, nearly flat, inequivalved shells. Pedicle notch very small. Characters very primitive. Lower Cambrian; India.

Trematis, Sharpe (*Orbicella*, d'Orb.) Ventral valve unevenly convex, more or less depressed over the posterior region. Pedicle fissure large, extending from the apex to the posterior margin. Dorsal valve evenly convex, and sometimes with incurved beak; posterior margin much thickened, and broadly grooved for the passage of the pedicle. Surface of both valves covered with punctures or small pittings arranged either in quincunx or in radiating rows. Ordovician and (?) Silurian; North America and (?) Europe.

Schizocrania, Hall and Whitfield. Ventral valve flat or concave, smaller than the dorsal, and bearing a deep and very broad triangular pedicle notch, which extends from just behind the beak to the posterior margin. Apex of notch occupied by a triangular plate, or listrium. Surface marked by concentric growth lines; no muscular impressions visible on the interior. Dorsal valve more or less convex, with beak marginal. External surface radially striated. On the interior, a low median ridge extends from the apex to beyond the centre of the valve; posterior adductor muscles strong; the anterior ones faint. Ordovician to Devonian; North America.

Oehlertella, Hall and Clarke (*Lingulodiscina*, Whitfield). Much like *Schizocrania*, but the ventral valve has concentric growth lines, and no radiating striae. Ventral pedicle area greatly elevated and transected by a narrow open fissure. Devonian to Lower Carboniferous; North America.

Schizobolus, Ulrich. Devonian; North America. (?) *Monobolina*, Salter.

Family 2. **Discinidae**. Gray.

Derived Discinacea with an open pedicle notch, in early life, in the posterior margin of the ventral valve, which is closed posteriorly during neanic growth, leaving a more or less long, narrow slit, partially closed by the listrium. Ordovician to Recent.

Orbiculoidea, d'Orbigny (Fig. 512). Shells inequivalved, sub-circular, or sub-elliptical in outline. Apices eccentric. Ventral valve depressed, convex, or flattened. Dorsal valve larger, usually depressed, conical. Pedicle furrow originating behind the apex, extending over a greater or lesser portion of the radius of the valve, and produced at the distal end into a short tubular sipho, emerging on the interior surface near the posterior margin. Surface with fine, crowded or distant, rarely lamellose, concentric lines occasionally crossed by radiating lines. Ordovician to Cretaceous; North and South America, Europe, and probably elsewhere.

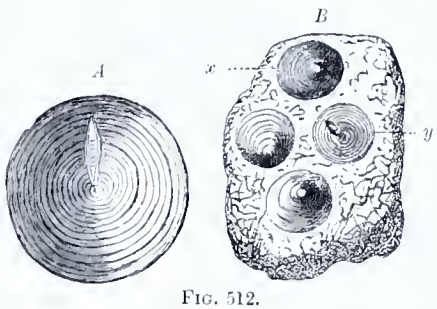


Fig. 512.

A, *Orbiculoidea Circe*, Bill. Ordovician; Belleville, Canada. Ventral valve, $^1/_1$ (after Billings). *B*, *O. nitida*, Phill. Sub-Carboniferous; Missouri. *x*, Dorsal; *y*, Ventral valve, $^1/_1$.

Discina, Lamarck. Very much like *Orbiculoidea*, but the pedicle emerges through the ventral shell antero-posteriorly, immediately beneath the beak, instead of through a sipho postero-anteriorly as in that genus. Recent.

Until recently, *Discina* embraced all fossil Discinoid shells, but at present this genus seems to be restricted to a single species, *D. striata*, living off Cape Palmas, West Africa.

Discinisca, Dall (Fig. 513). Like *Orbiculoidea*, but with a small septum, as in *Discina*, behind which is an impressed area, externally concave and internally elevated. This is perforated by a longitudinal fissure, extending from a short distance behind the septum nearly to the posterior margin. Tertiary to Recent; North America and Europe.

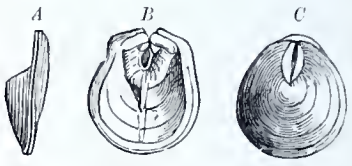


Fig. 513.

Discinisca lamellosa, Brod. Recent; Peru. *A*, Side-view. *B*, Interior of ventral valve. *C*, Exterior of same.

Schizotreta, Kutorga. Ordovician and Silurian; Russia and North America.

Lindstroemella and *Roemerella*, Hall and Clarke, are genera related to *Orbiculoidea*. Devonian; North America.

Superfamily 3. **CRANIACEA**. Waagen.

Cemented calcareous Neotremata without pedicle or anal openings at maturity. Ordovician to Recent.

Family 1. Craniidae. King.

Crania, Retzius (Fig. 514). Shell inequivalve, sub-circular in outline. In the interior of both valves are two pairs of large adductor scars, the posterior of which are widely separated and often strongly elevated on a central

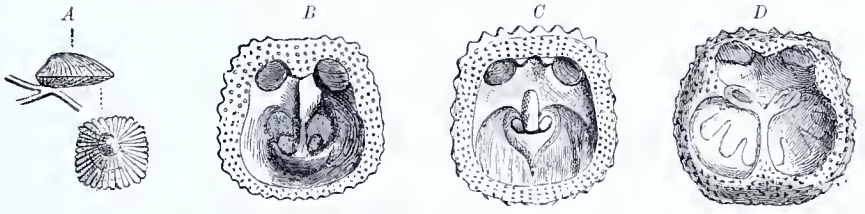


Fig. 514.

Crania Ignabergensis, Retzius. Uppermost Cretaceous; Ignaberga, Scania. *A*, Profile and dorsal aspect of shell, 1/1. *B*, *C*, Interior of ventral valve. *D*, Interior of dorsal valve, enlarged.

callosity. Impressions of the pallial genital canals coarsely digitate. Ordovician to Recent; maximum development in Ordovician and Cretaceous.

Craniella, Oehlert. Large Cranias with S-shaped vascular impressions. (?) Ordovician and Devonian; North America and Europe.

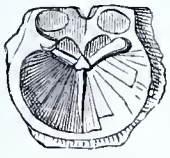


Fig. 515.

Craniscus velata, Quenst. Upper Jura; Oerlinger Thal, Würtemberg. Interior of ventral valve, 1/1 (after Quenstedt).

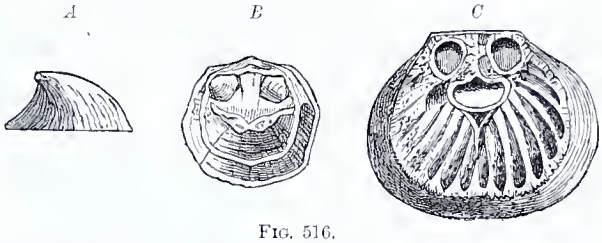


Fig. 516.

Ancistrocrania Parisiensis, Defr. Upper Cretaceous; France. *A*, Profile of dorsal valve. *B*, Interior of same. *C*, Interior of ventral valve, 1/1.

Craniscus, Dall (Fig. 515). Ventral interior divided by septa into three cavities. Jurassic; Europe.

Ancistrocrania, Dall (Fig. 516). Dorsal valve with two muscular fulcra. Cretaceous; Europe.

Pholidops, Hall (*Craniops*, Hall). Biconvex and but slightly attached Cranias. Ordovician to Carboniferous; North America, England, Gottland.

Pseudocrania, M'Coy (*Palaeocrania*, Quenstedt). Radially striated shells much like *Pholidops*. Ordovician; Europe.

Cardinocrania, Waagen. Permian of India.

Order 3. PROTREMATA. Beecher.

Articulate Brachiopoda, with the pedicle opening restricted to the ventral valve throughout life or during early growth. Prodeltidium originating on the dorsal side of the body wall in the Cephalula stage, and later anchylosed to the ventral shell, thus initiating the development of a deltidium. Pedicle aperture modified by the deltidium. Brachia unsupported by a calcareous skeleton except in Pentameracea, where there are crura.

Superfamily 1. STROPHOMENACEA. Schuchert.

Primitive Protremata without spondylia and cruralia. Cambrian to Recent.

Family 1. Kutorginidae. Schuchert.

Primitive Strophomenacea with incipient cardinal areas, great delthyrium and very rudimentary articulating processes and deltidium. Cambrian.

Kutorgina, Billings. *K. cingulata*, as redefined by Walcott, from the American Lower Cambrian, is the only species positively known to belong to this family. *Schizopholis*, Waagen, of the Lower Cambrian in India, and *Volborthia*, Möller, of the Ordovician, may also possibly find a place here.

? Family 2. Eichwaldiidae. Schuchert.

Primitive or aberrant, rostrate Strophomenacea, with narrow lateral grooves and ridges for articulation. Delthyrium closed by a concave plate (? deltidium). Pedicle emerging through the ventral umbone and moving with growth anteriorly by resorption through the shell, as in Siphonotretidae. Ordovician and Silurian.

Eichwaldia, Billings. The single species of this genus has a smooth exterior. Ordovician; North America.

Dictyonella, Hall (*Eichwaldia*, auct.) Exterior surface of valves pitted in quincunx, resembling *Trematis*. Silurian; North America, England, Bohemia, and Gottland.

Family 3. Billingsellidae. Schuchert.

Strophomenacea with well-developed cardinal areas and deltidium. Cardinal process obsolete or very rudimentary. Articulation fairly well developed. Cambrian.

Billingsella, Hall and Clarke (*Protorthis*, H. and C.) This is the only known genus of the family, and contains a number of the oldest well-developed species of *Protremata*. Cambrian; North America.

Family 4. Strophomenidae. King.[1]

Strophomenacea with well-developed cardinal areas, deltidium, chilidium, cardinal, and articulating processes. Ordovician to Permian.

Rafinesquina, Hall and Clarke (Fig. 517). Shells normally concavo-convex dorso-ventrally. Striae alternating in size, and crossed by finer concentric growth lines. Muscular area of ventral valve consisting of two broad flabellate diductor scars enclosing an elongate adductor. In the dorsal valve, the bilobed cardinal process is low; the posterior arborescent adductor scars well defined. Vascular and ovarian markings often well indicated. Ordovician; North America and Europe.

[1] [According to J. M. Clarke, a separation into groups of the genera here included under one family is advisable, according as the shell is normally convex, or reversed convex. The habit of reversion, originating in the unequal growth of the two valves, characterises a large number of forms, which stand in a notable degree in successive genetic relationships; while their affinities with the normally convex forms are less palpable. This author is in favour of restricting the *Strophomenidae* so as to include only those genera in which the shell is usually reversed convex, and employing the family term *Leptaenidae* for those having normally convex shells.—Trans.]

Stropheodonta, Hall. Shells very much like *Rafinesquina*, but with the cardinal margins finely denticulate and the deltidium flat or not discernible. Silurian and Devonian; North America and Europe.

Leptostrophia, Hall and Clarke; *Douvillina*, Oehlert and *Brachyprion*, Shaler, are sub-genera of *Stropheodonta*. Silurian and Devonian.

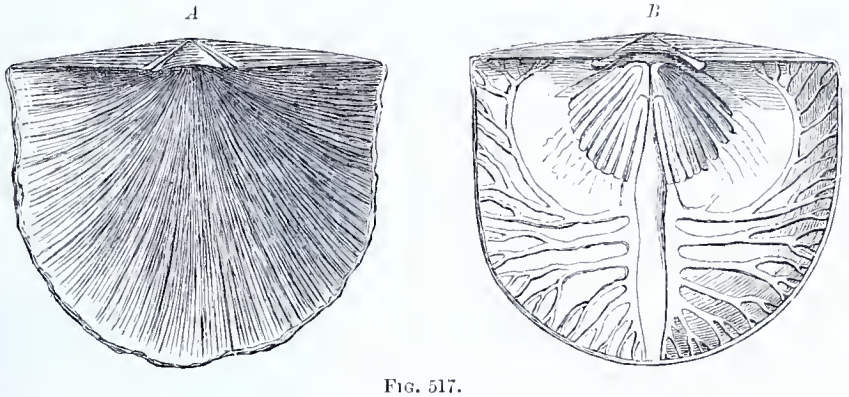


FIG. 517.

A, *Rafinesquina alternata*, Conrad sp. Ordovician; Cincinnati, Ohio. 1/1. *B*, *R. expansa*, Sow. sp. Interior of ventral valve, showing muscular and vascular impressions.

Pholidostrophia, Hall and Clarke. Smooth or squamose, nacreous small *Stropheodontae*. Devonian; North America and Europe.

Strophonella, Hall (*Amphistrophia*, Hall and Clarke). Resupinate *Stropheodontae*. Silurian and Devonian; North America and Europe.

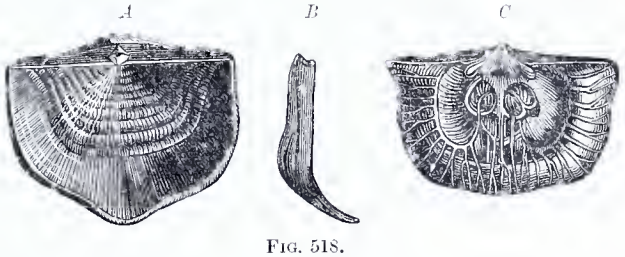


FIG. 518.

Leptaena rhomboidalis, Wahlenb. sp. Silurian; Gottland. *A*, *B*, Dorsal aspect and profile. *C*, Interior of dorsal valve.

Leptaena, Dalman (*Leptagonia*, M'Coy), (Fig. 518). Shells having the characters of *Rafinesquina*, but the flatter portions of the valves with corrugations and wrinkles. Where these cease, the shells are more or less abruptly and often rectangularly deflected. Ordovician to Carboniferous.

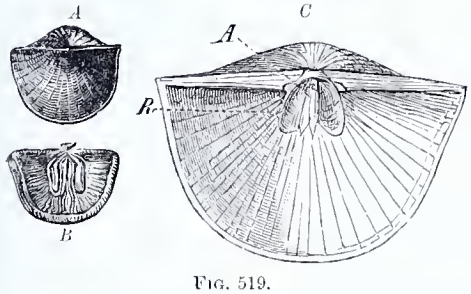


FIG. 519.

Plectambonites transversalis, Dalm. sp. Silurian; Gottland. *A*, Dorsal aspect, 1/1. *B*, Interior of dorsal valve, 1/1. *C*, Ventral valve, 3/1. (*A*, Adductors; *R*, Divaricators).

Cadomella, Munier-Chalmas. Similar to *Rafinesquina*, but in the ventral valve between the divergent teeth there is a bowl-shaped muscular apophysis for the attachment of accessory diductors. The prominent socket walls of the dorsal valve continued into curved crural apophyses, which sometimes terminate freely.

Plectambonites, Pander (*Leptaena*, Davidson and auct.), (Fig. 519). Ordovician and Silurian; North America and Europe.

Leptella, Hall and Clarke. Primitive *Plectambonites*. Upper Cambrian and Lower Ordovician; North America and England.

Leptaenisca, Beecher. Ventrally cemented shells having some of the characters of *Plectambonites*. Markings of the fleshy arms are retained on the dorsal shell. Silurian; North America.

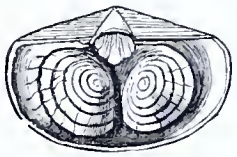


Fig. 520.

Davidsonia Bouchardiana, de Kon. Devonian; Eifel. Ventral valve with spiral markings, 2/1.

Christiania, Hall and Clarke. Differs from *Leptaenisca* in having prominent longitudinal ridges instead of spiral markings on the dorsal interior. Basal Devonian; North America, England, and Russia.

Davidsonia, Bouchard (Fig. 520). Thick *Leptaenisca*-like shells, with spiral markings of the fleshy arms strongly impressed on both valves. Devonian; England, Belgium, and Russia.

Strophomena, Blainville. Shells like *Rafinesquina*, but resupinate, or with the relative convexity of valves reversed, and the ventral muscular area sharply limited by an elevated margin. Ordovician; America and Europe.

Orthothetes, Fischer (Figs. 521, 522). Much like *Strophomena*. Shell plano-convex or biconvex, but becoming concavo-convex with age. Surface covered with radiating striae, which are convoluted by sharp concentric lines. Hinge-line as long or longer than the greatest width of the shell. Cardinal area of ventral valve prominently developed; dorsal area narrow. Cardinal process united to crural plates, the whole forming a vertical sub-crescentic process. Muscular impressions flabelliform. Silurian to Carboniferous; North and South America, Europe, and India.

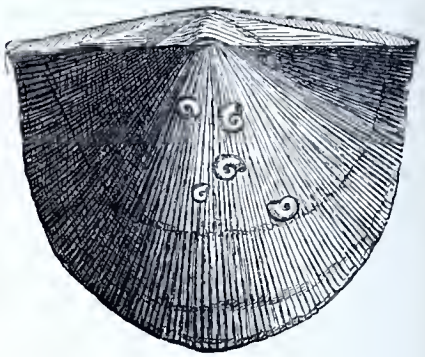


Fig. 521.

Orthothetes umbraculum, Schloth. sp. Devonian; Gerolstein, Eifel. Natural size.

Hipparionyx, Vanuxem. Like *Orthothetes*, but with the muscular areas much larger and no dorsal cardinal area. Lower Devonian; North America.

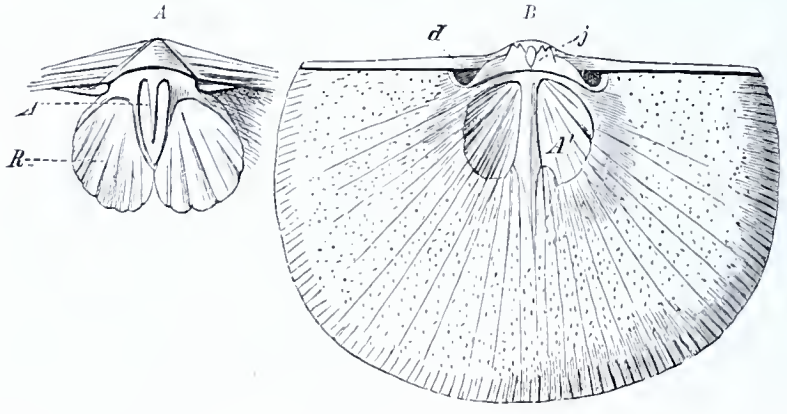


Fig. 522.

Orthothetes crenistria, Phill. Carboniferous Limestone; Wexford. *A*, Muscular portion of ventral valve. *B*, Interior of dorsal valve. (*A*, *A'*, Adductors. *R*, Diductors; *j*, Cardinal process; *d*, Dental sockets), (after Davidson).

Kayserella, Hall and Clarke. Small *Orthothetes*-like shells, with a very high dorsal median septum. Devonian; Germany.

Derbya, Waagen. Like *Orthothetes*, with a high median septum in the ventral

apex and muscular area, and usually ventrally cemented. Carboniferous; North and South America, Europe, India, and Russia.

Streptorhynchus, King. Very much like *Derbya*, but without the ventral septum. Beak acute, incurved, or distorted. Carboniferous and Permian; America, Europe, and India.

Meekella, White and St. John. Very biconvex shells, with the teeth of the ventral valve supported by septiform dental lamellae, which reach to the bottom of the umbonal cavity, and extend forward for one-third or one-half the length of the shell. Surface of valves with coarse costae and fine radiating, often plumose, striae. Upper Carboniferous; North America, Russia, India, and China.

Triplecia, Hall (*Dicraniscus*, Hall). Trilobate, unequally biconvex, short-hinged shells. Cardinal process long, erect, and bifurcate. Surface of valves usually smooth, but sometimes striated radially. Ordovician and Silurian; North America, England, and Bohemia.

Mimulus, Barrande. Like *Triplecia*, but with the median fold on the ventral valve. No external evidence of a deltidium. Silurian; Bohemia and North America.

Streptis, Davidson. Like *Triplecia*, but biconvex and bilaterally unsymmetrical. Exterior with lamellar concentric shell expansions. Silurian; England, Gottland, and North America.

? *Orthidium*, Hall and Clarke. Ordovician; North America.

Family 5. Thecidiidae. Gray.

Cemented Strophomenacea, in which the interior of the shell is impressed with variously indented brachial furrows. Carboniferous to Recent.

This family was formerly associated with the *Terebratulidae*. Beecher has shown, however, that brachial supports are wanting, and that a true deltidium is present.

Lyttonia, Waagen (*Leptodus*, Kayser). Very large, highly inequivalved, irregular shells, frequently with broad lateral expansions. Numerous, laterally directed, brachial ridges in the ventral valve, with corresponding divergent grooves in the median region of the dorsal valve. Carboniferous; China and India.

Oldhamia, Waagen (Fig. 523). Differs from *Lyttonia* in that the ventral valve is sub-hemispherical with the incurved apex covered by a callosity, as in *Bellerophon*. Carboniferous; India and China.

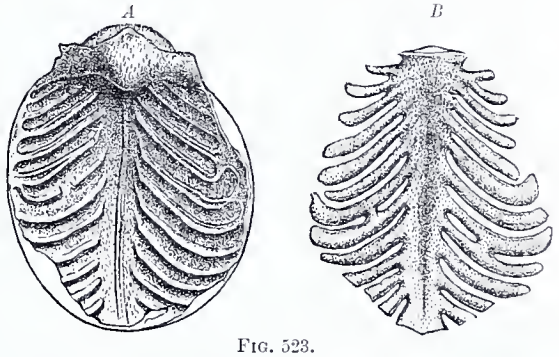


Fig. 523.

Oldhamia decipiens, Waagen. Productus Limestone; Salt Range, East India. *A*, *B*, Interior of ventral and dorsal valves, respectively (after Waagen).

Thecidea, Defrance (*Thecidium*, Sowerby), (Fig. 524). Dorsal brachial impressions with three pairs of symmetrical lobes, radially directed. Cretaceous.

Thecidea and the following genera of the family *Thecidiidae* comprise for the most part small, sometimes extremely minute forms, represented from the Trias to the present day; the climax of diversity occurred in the Cretaceous.

Lacazella, Munier-Chalmas (Figs. 525, 526). Dorsal brachial impressions

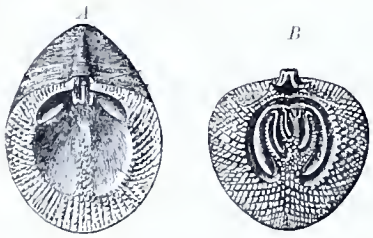


Fig. 524.

Thecidea papillata, Schloth. Upper Cretaceous; Ciply, Belgium. *A*, *B*, Interior of ventral and dorsal valves, respectively, $^2/_1$ (after Woodward).

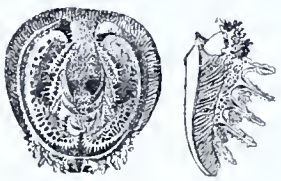


Fig. 525.

Lacazella vermicularis, Schloth. sp. Upper Cretaceous; Maestricht. Dorsal valve, $^2/_1$ (after Suess).

Fig. 526.

Lacazella Mediterranea, Risso. Recent. Interior of dorsal valve showing brachia, $^2/_1$ (after Woodward).

with two or three unequal pairs of lobes, medially directed. Jurassic to Recent; Europe.

Thecidiopsis, Munier-Chalmas (Fig. 527). The two, large, dorsal, brachial impressions each have four pairs of lobes laterally and medially directed. Cretaceous; Europe.

Thecidella, Munier-Chalmas. Dorsal brachial impressions simple, anteriorly directed. Jurassic; Europe.

Eudesella, Munier-Chalmas. Transverse shells in which the dorsal brachial

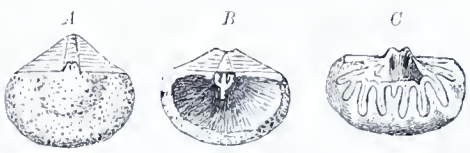


Fig. 527.

Thecidiopsis digitata, Goldf. Greensand; Essen on the Rhine. *A*, Dorsal aspect. *B*, *C*, Interior of ventral and dorsal valves, respectively, $^1/_1$.

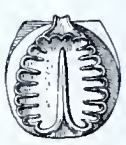


Fig. 528.

Pterophloios Emmrichi, Gümbel. Rhaetic; Kössen, Tyrol. Interior of dorsal valve, $^1/_1$.

impressions have three pairs of simple lobes antero-laterally directed. Jurassic; Europe.

Pterophloios, Gümbel (*Bactrynium*, Emmrich), (Fig. 528). Dorsal brachial impressions with about ten laterally directed lobations. Alpine Rhaetic.

Davidsonella, Munier-Chalmas. Elongate shells with the long, narrow, dorsal, brachial impressions simple and antero-laterally directed. Jurassic; Europe.

Family 6. **Productidae.** Gray.

Strophomenacea with hollow anchoring spines. Silurian to Permian.

Chonetes, Fischer (Fig. 529). Shell transversely elongate, semi-circular in outline, normally concavo-convex, sometimes plano-convex. Upper margin of cardinal area in ventral valve bearing a single row of hollow spines; these are prolongations of tubes which penetrate obliquely the substance of the shell along the hinge-line. Teeth strong. Cardinal process of dorsal valve divided by a narrow median and two broader lateral grooves. Brachial impressions more or less distinct. External surface usually covered with radiating striae, rarely smooth or concentrically rugose. Silurian to Permo-Carboniferous.

Anoplia, Hall and Clarke. Smooth or squamose shells like *Chonetes*, supposed to be without cardinal spines. Lower Devonian.

Chonostrophia, Hall and Clarke. Like *Chonetes*, but with the shell reversed or concavo-convex. Lower and Middle Devonian; North and South America.

Chonetella, Waagen. Upper Carboniferous; India. *Chonetina*, Krotow. Permian; Russia.

Chonopectus, Hall and Clarke. *Chonetes*-like shells, but cemented ventrally to extraneous objects. External surface reticulated by a double, oblique series of concentric lines and fine radiating striae. Lower Carboniferous; North America.

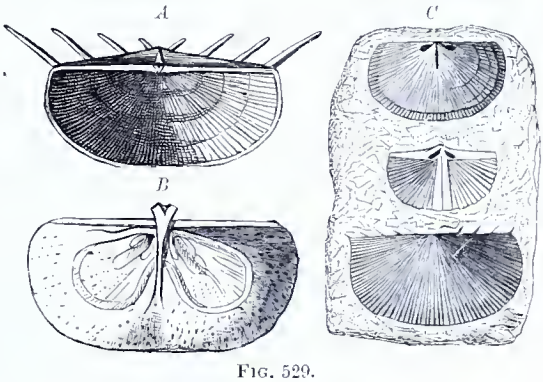


Fig. 529.

A, *Chonetes striatella*, Dalm. sp. Silurian; Gottland. 1/1. *B*, Interior of dorsal valve of *Chonetes* (after Davidson). *C*, *C. sarcinulata*, de Kon. Devonian; Coblenz. 1/1.

Strophalosia, King (*Orthothrix*, Geinitz; *Leptaenalosia*, King), (Fig. 530). Shell Productoid in general form, cemented by the ventral umbo. Both valves with well-defined area and deltidium. Ventral valve with two prominent teeth unsupported by lamellae. Muscular impressions small; brachial ridges distinct. Surface of ventral valve covered with spines; that of the dorsal valve either spinous, lamellose, or smooth. Middle Devonian to Permian; Europe, India, North and South America.

Aulosteges, Helmersen. Much like *Strophalosia*, but not cemented by the ventral umbo; deltidium covered with small spinules and the surface of both valves thickly set with spines. Permian; Russia and India.

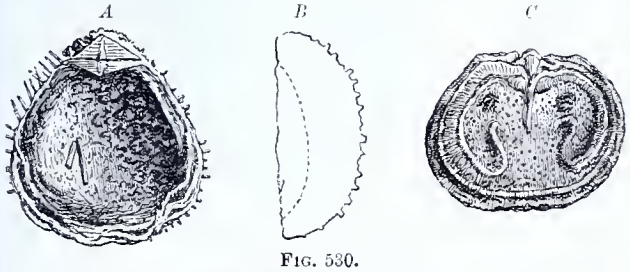


Fig. 530.

Strophalosia Goldfussi, Münst. sp. Permian; Gera, Reuss. *A*, Dorsal aspect. *B*, Profile. *C*, Cast of dorsal valve with brachial impressions. Natural size.

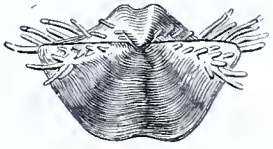


Fig. 531.

Productus horridus, Sow. Permian; Gera, Reuss. 1/4.

Productella, Hall. Shells small, Productoid, with narrow cardinal areas in both valves. Ventral valve with small teeth; dorsal valve with sockets and crural plates. Brachial impressions distinct. Devonian.

Productus, Sowerby (*Pyxis*, Chemnitz; *Arbusculites*, Murray; *Protonia*, Linck; *Marginifera*, Waagen), (Figs. 531, 532). Shell without functional pedicle, probably anchored by the ventral spines; concavo-convex, valves usually produced anteriorly; outlines semi-circular, sometimes transversely elongate. External surface usually with more or less prominent radiating ribs, which are crossed by concentric lines or wrinkles; rarely smooth or finely striated. Cardinal areas, teeth, sockets, and crural plates absent or rudimentary. Ventral valve convex, sometimes geniculated; occasionally with median sinus. Muscular impressions consisting of two dendritic adductors and a pair of broadly flabellate, striate diductors; traces of spiral or brachial cavities occasionally

present in the pallial region. Cardinal process strong, curved, or erect, extending far above the hinge-line. Brachial ridges well defined. Extraordinarily abundant in Carboniferous and Permian. Distribution general.

P. giganteus is the largest Brachiopod known, sometimes attaining a width of nearly one foot.

Proboscidella, Oehlert. Valves very unequal; dorsal valve small, concave, operculiform; ventral valve larger, convex, furnished with two lateral expansions which bend downward to meet the margins of the dorsal valve, and an

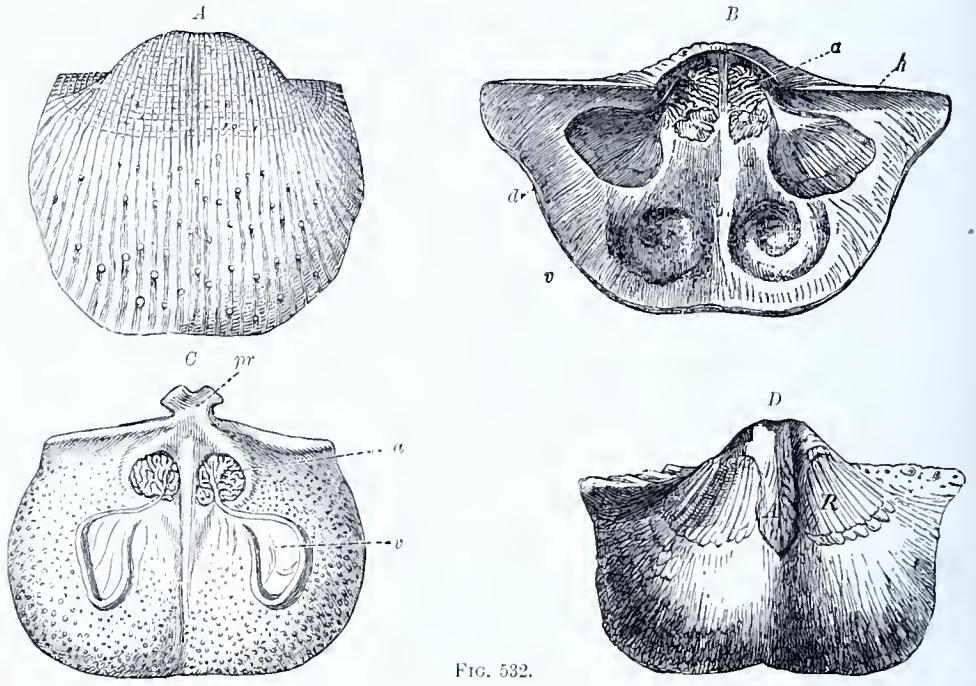


FIG. 532.

A, *Productus semireticulatus*, Martin. Carboniferous Limestone; Visé, Belgium. 1/1. *B*, *P. giganteus*. Martin sp. Same horizon; England. Interior of dorsal valve (after Woodward). *C*, *D*, *P. horridus*, Sow. Permian; Prussia and England. 1/1. *C*, Interior of dorsal valve. *D*, Cast of ventral valve (*A*, Adductors; *R*, Diductors; *pr*, Cardinal process; *h*, Hinge-line; *v*, Brachial impressions).

anterior expansion, which is produced forward into one, or occasionally two, long, cylindrical tubes. Carboniferous; Europe and North America.

Etheridgina, Ochlert. Shell very small, nearly as broad as long, and attached to foreign bodies, notably Crinoids, by the spines of the ventral valve. Dorsal valve with a small beak; surface ornamented by concentric flexuous plications bearing a few scattered spines. Carboniferous; Scotland.

? *Daviesiella*, Waagen. Shell Productoid, but without spines and well-developed cardinal area and teeth. England.

? *Aulacorhynchus*, Dittmar (*Isogramma*, Meek and Worthen). Very large, transverse, thin shells with a ventral platform. Exterior surface with numerous, regular, continuous, concentric ridges. Upper Carboniferous; Europe and North America.

Family 7. **Richthofenidae.** Waagen.

Strophomenacea, probably derived through the Productidae, and remarkably modified by ventral cementation. The form is that of Cyathophylloid corals with an operculiform dorsal valve. Shell structure cystose.

Richthofenia, Kayser (Fig. 533). These most remarkable modified Brachiopods are found in the Permo-Carboniferous of China and India.

Fig. 533.

Richthofenia Lawrenciana, Waagen. Permo-Carbon.; Salt Range. Vertical section of ventral valve (after Waagen).

Family 8. **Orthidae.** Woodward.

Strophomenacea usually with large open delthyria; deltidium developed only in younger growth stages. Ordovician to Permian.

Orthis, Dalman (*Orthambonites*, Pander), (Figs. 534-536). Shell sub-quadrate to sub-circular in outline; surface covered with radiating striae or costae. Valves more or less convex; the small or dorsal valves sometimes nearly flat or slightly concave. Cardinal areas well developed in both valves, and usually divided by open delthyria. Hinge-teeth large, and supported by well-developed dental plates. Dental sockets of dorsal valve deep, their inner walls supporting short divergent crura. Median ridges frequently present in both valves. Vascular markings often retained. Ordovician to Carboniferous; particularly abundant in the Ordovician and Silurian, which have alone yielded about 400 species. Distribution general.

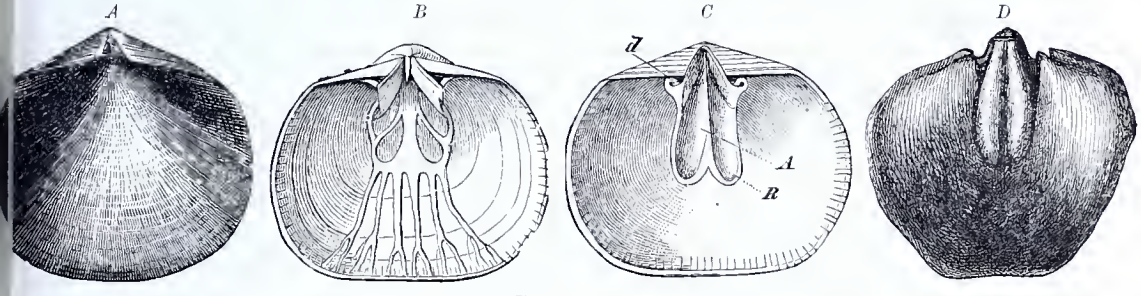


Fig. 534.

A-C, *Orthis* (*Schizophoria*) *striatula*, Schloth. sp. Devonian; Gerolstein, Eifel. *A*, Dorsal aspect. *B*, Interior of dorsal valve. *C*, Interior of ventral valve. *D*, *Orthis vulvaria*, Schloth. Spiriferensandstein; Niederlahnstein, Nassau. (All figures of the natural size.)

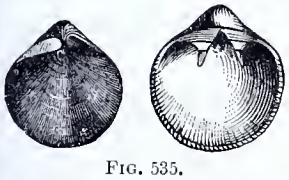


Fig. 535.

Orthis (*Dalmanella*) *elegantula*, Dahm. Silurian; Gottland. 1/1.

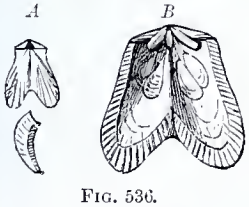


Fig. 536.

Orthis (*Bilobites*) *biloba*, Lin. Silurian; Gottland. *A*, Shell, 1/1. *B*, Interior of dorsal valve, 2/1.

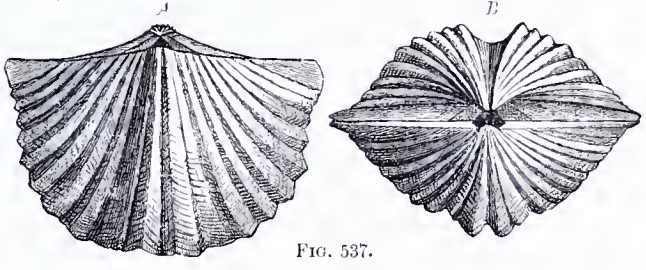


Fig. 537.

Platystrophia lynx, Eichw. Ordovician; Cincinnati, Ohio. 1/1.

This genus has been recently divided by Hall and Clarke into fifteen sub-genera, as follows:—*Orthis* s.s., *Plectorthis*, *Dinorthis*, *Plaesiomys*, *Hebertella*, *Orthostrophia*, *Platystrophia*, King (Fig. 537), *Heterorthis*, *Bilobites*, Linné (Fig. 536), *Dalmanella* (Fig. 535), *Rhipidomella*, Oehlert, *Schizophoria*, King (Fig. 534), *Orthotichia*, *Enteletes*, Fischer de Waldheim, and *Orthotropia*.

Superfamily 2. **PENTAMERACEA.** Schuchert.

Derived Protremata with spondylia, to which are attached the adductor, diductor, and ventral pedicle muscles. Cruralia commonly present. Ordovician to Permian.

Family 1. **Clitambonitidae.** Winchell and Schuchert.

Primitive Pentameracea with long, straight cardinal areas and a well-developed deltidium. No cruralium. Ordovician to Devonian.

Clitambonites, Pander (*Orthisina*, d'Orb., *Pronites*, *Hemipronites*, and *Gonambonites*, Pander), (Fig. 538). Valves convex or sub-pyramidal. Hinge-line straight, forming the greatest diameter of the shell. Cardinal area of the ventral valve high; delthyrium broad, and covered by a perforate deltidium; that of the dorsal valve covered by a chilidium. Dental lamellae of ventral valve very strongly developed, uniting to form a concave spatulate plate or spondylium. This plate serves for the attachment of muscles, and is supported by a median septum extending for about one-half the length of the valve. External surface radially striated. Shell substance impunctate. Ordovician; Russia, England, and North America.

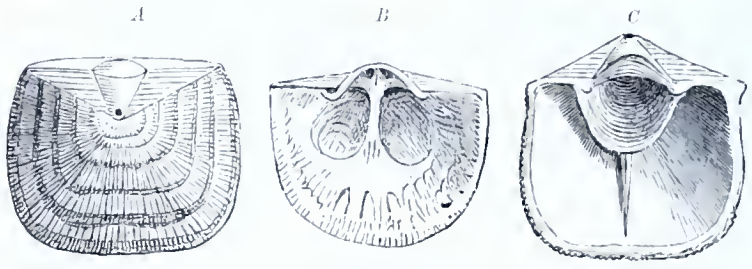


Fig. 538.

A, *Orthisina adscendens*, Pand. Ordovician; Pawlowsk, near St. Petersburg. 1/1. *B*, *C*, *O. squamata*, Pahlen. Ordovician; Kuckers, Esthonia. *B*, Interior of dorsal valve, showing edge of the chilidium. *C*, Interior of ventral valve, showing spondylium, septum, and deltidium (after Pahlen).

Polyfoechia, Hall and Clarke. Like *Orthisina*, but with the spondylia supported by three septa, thus dividing the umbonal cavity of the ventral valve into five chambers. Ordovician; North America.

Scenidium, Hall (*Mystrophora*, Kayser). Small Orthisinoid shells with the delthyrium partially closed by a concave imperforate deltidium. Cardinal process extending as a median septum throughout the length of the shell. The septum is sometimes greatly elevated anteriorly in Devonian species. Ordovician to Devonian; North America, Europe, and the Urals.

Family 2. **Syntrophiidae.** Schuchert.

Primitive Pentameracea with long, straight cardinal areas, deltidia, and cruralia. Lowest Ordovician.

Syntrophia, Hall and Clarke. Transverse, straight-hinged, primitive Pentameroids. North America.

Family 3. **Porambonitidae.** Davidson.

Pentameracea intermediate in structure between the Syntrophiidae and Pentameridae; the deltidium and the straight cardinal areas of the former family tending to obsolescence, particularly the deltidium. The Porambonitidae approach the latter

family in tending to develop a rostrate shell. Cruralium present. Ordovician to Lower Devonian.

Camarella (Billings), Hall and Clarke. Small smooth shells with a few low plications and without cardinal areas. Dorsal valve at maturity most convex. Spondylium well defined. Cruralium very small, supported by a long septum. Ordovician; North America and (?) England.

Parastrophia, Hall and Clarke. Much like *Camarella*, but with a moderately long, straight, cardinal line, and no cardinal area. Dorsal umbo conspicuous, projecting beyond that of the ventral valve. Ordovician and Silurian; North America and England.

Anastrophia, Hall (*Brachymerus*, Shaler, non Dej.) Much like *Parastrophia*, but with the dorsal umbo more prominent and the valves with numerous sharp

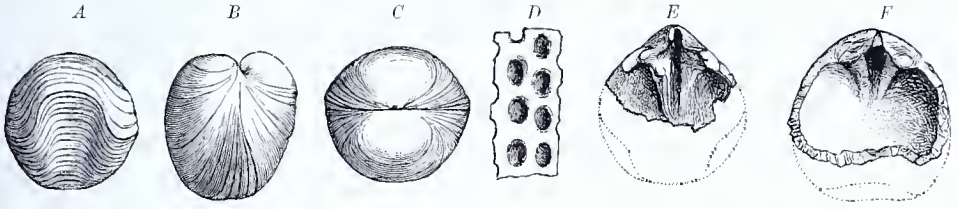


FIG. 539.

Porambonites aequirostris, Schloth. sp. Ordovician (Vaginatenkalk); St. Petersburg. *A-C*, Anterior, lateral, and posterior aspects of shell, 1/1. *D*, Punctate surface, magnified. *E, F*, Interior of ventral and dorsal valves, respectively.

plications extending to the beaks. Silurian and Lower Devonian; North America, England, and Gottland.

Porambonites, Pander (*Isorhynchus*, King), (Fig. 539). Shells similar to *Parastrophia* in form, but without plications, and with obtusely triangular areas in both valves. Shells thick, variously pitted externally. Ordovician; Russia.

Noetlingia, Hall and Clarke. Exterior like *Porambonites*, but with long, straight, hinge-line, prominent cardinal areas, and perforate beaks. Ordovician; Russia.

? *Lycophoria*, Lahusen. Russia and Scandinavia.

Family 4. **Pentameridae.** M'Coy.

Rostrate Pentameracea rarely with straight cardinal areas. Deltidium commonly absent, but sometimes present as a concave plate, being the reverse of the ordinary form of the deltidium and due to the incurved beaks. Cruralium present. Silurian to Permian.

Conchidium, Linné (*Gypidia*, Dalman; *Antirhynchonella*, Quenstedt; *Zdimir*, Barrande), (Fig. 540). Shell strongly inequivalve, biconvex, with highly arched ventral valve. Surface numerously plicated. Spondylium narrow and deep, and supported by a high vertical septum of variable length. A small cardinal process present. Silurian and Devonian; distribution general.

Stricklandinia, Billings. Similar to *Conchidium*, but with a straight hinge-line and no prominent arched ventral beak. Spondylium small and short, supported by a short median septum. Silurian; North America, England, and Gottland.

Pentamerus, Sowerby (*Pentastère*, Blainville). Like *Conchidium*, but with

smooth shells, or sometimes with a few broad and obscure radiating undulations. Silurian; distribution probably general.

Capellinia, Hall and Clarke. Like *Pentamerus*, but with the relative convexity of the valves reversed. North America.

Clorinda, Barrande (*Barrandella*, Hall and Clarke). Small galeatiform

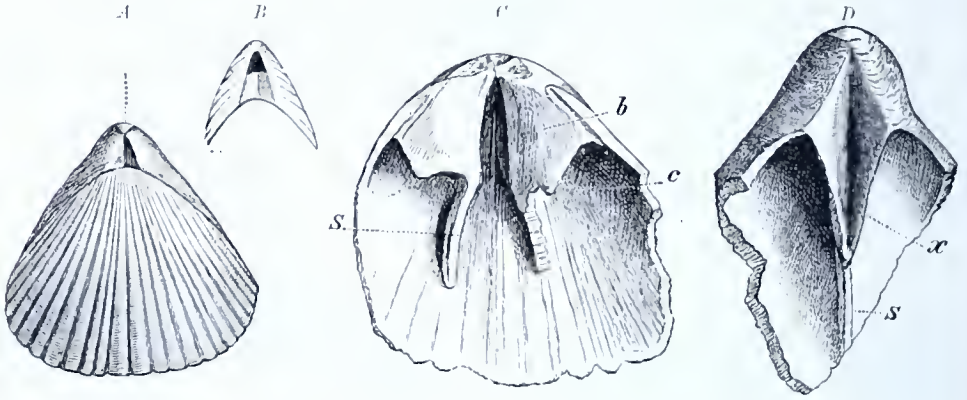


Fig. 540.

Conchidium biloculare, Linn. Silurian; Gottland. *A*, Shell of the natural size. *B*, Beak showing concave deltidium. *C*, *D*, Interior of dorsal and ventral valves, respectively (*x*, Spondylium; *S*, Median septum of ventral valve, Fig. *D*; *b*, Dental lamellae; *c*, Crura; *S*, Septum-like supports, Fig. *C*).

Pentameroids usually with smooth shells, rarely plicate. Spondylium without a supporting septum. Silurian; North America and Europe.

Pentamerella, Hall. Much like *Clorinda*, but with strong plications and a narrow cardinal area. Devonian; North America.

Gypidula, Hall (*Sieberella*, Oehlert), (Fig. 541). Galeatiform Pentameroids, with the median sinus on the dorsal, and the fold on the ventral valve. In

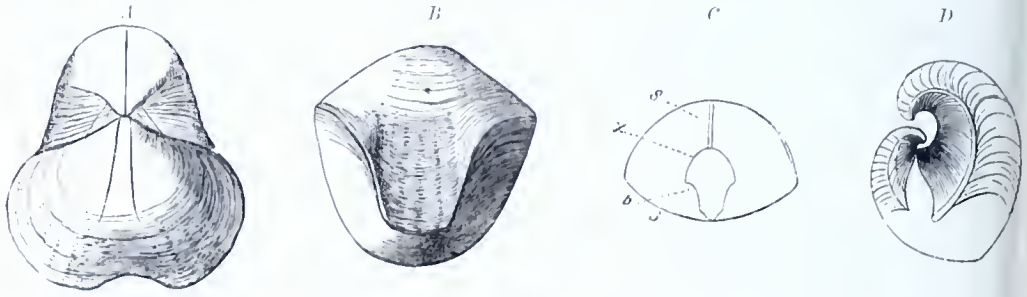


Fig. 541.

A-C, *Gypidula galeata*, Dalm. sp. Devonian; Gerolstein, Eifel. *A*, Dorsal aspect, 1/1. *B*, Anterior aspect. *C*, Transverse section below the hinge-line. (Lettering the same as in Fig. 540 *C*, *D*.) *D* *Conchidium Knightii*, Sow. Silurian; England. 1/2.

Sieberella there is no cardinal area, but in typical *Gypidula* there is a well-defined, cross-striated, cardinal area. Surface smooth or plicate. Silurian and Devonian; North America and Europe.

Amphigenia, Hall (*Enantiosphen*, Whidborne). Elongate-ovate, high-shouldered shells without median fold or sinus. Surface with concentric growth varices and faint radial striae. Dorsal valve with a large sub-quadrate hinge-plate perforated by the visceral foramen and without a cruralium. Middle Devonian; North and South America, France, and Germany.

Camarophoria, King (Fig. 542). Shells Rhynchonelliform with the surface

more or less strongly plicated. Spondylium supported by a long median septum. Devonian to Permian; Europe, India, and North America.

Camarophorella, Hall and Clarke. Biconvex, sub-circular *Camarophoriae*, but without sinus, fold, and plications. Lower Carboniferous; North America.

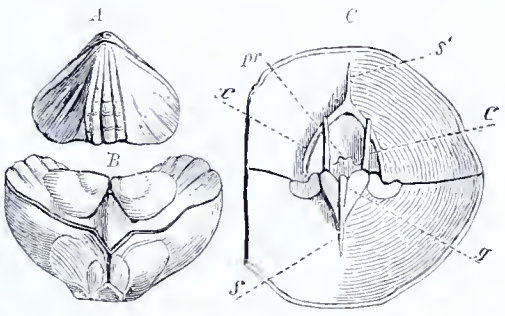


FIG. 542.

Camarophoria Schlotheimi, v. Buch. Permian; Gera, Reuss. *A*, Shell, 1/1. *B*, Cast. *C*, Interior of shell, enlarged (*pr*, Cardinal process; *c*, Crura; *s*, Spondylium; *g*, Dental plates of dorsal valve; *s*, *s'*, Median septa).

Order 4. TELOTREMATA. Beecher.

Articulate Brachiopoda, with the pedicle opening shared by both valves in nepionic and early neanic stages, usually confined to one valve in later stages, and becoming more or less modified by deltidial plates in ephebic stages. Brachia supported by calcareous crura, loops, or spiralia. Prodeltidium absent.

Superfamily 1. RHYNCHONELLACEA. Schuchert.

Rostrate, primitive Telotremata, with or without crura. Cambrian to Recent.

Family 1. Protorhynchidae. Schuchert.

Primitive Rhynchonellacea without deltidial plates or crura. Cambrian and Ordovician.

Protorhyncha, Hall and Clarke. Biconvex *Rhynchonellae* with the fold and sinus ill-defined. No cardinal process or dorsal median septum. Surface with low radial plications. Ordovician.

There are smooth-shelled, very primitive *Rhynchonellae* in the American Lower Cambrian belonging to this family.

Family 2. Rhynchonellidae. Gray.

Rhynchonellacea with crura of greater or lesser length. Ordovician to Recent.

Orthorhynchula, Hall and Clarke. *Rhynchonellae* with short straight hinge-line and cardinal areas in both valves, bisected mesially by open delthyria. External surface plicate. Teeth unsupported by dental lamellae. A linear cardinal process present. Ordovician; North America.

Rhynchotrema, Hall (*Stenochisma*, Conrad, 1839; and Hall, 1867). Thick-shelled, often gibbous *Rhynchonellae* with prominent, thick, concave deltidial plates. Dorsal valve with a thick median septum, upon which rests a linear cardinal process. Crural plates very broad and stout. Ordovician to Devonian; North America.

Rhynchotreta, Hall. Trihedral *Rhynchonellae* with the ventral beak acuminate and produced. Pedicle foramen apical, the delthyrium being completely closed by the deltidial plates. Dental lamellae and cardinal process present. The prominent dorsal median septum separates posteriorly, each

branch supporting one process of the divided hinge-plate. Silurian; North America and Europe.

Camarotoechia, Hall and Clarke (*Plethorhyncha*, H. and C.) *Rhynchonellae* with the dorsal median septum bearing posteriorly an elongate cavity. Cardinal process absent; dental lamellae present. Ordovician to Carboniferous; North America and Europe.

Leiorhynchus, Hall. Like *Camarotoechia*, but with the plications on the lateral slopes usually faint or obsolete. Devonian to Carboniferous.

Wilsonia, Kayser (*Uncinulina*, Bayle). Sub-cuboidal or sub-pentahedral *Rhynchonellae* with the low plications marked anteriorly by fine median lines. Dental lamellae present. No cardinal process. Silurian and Devonian; North America and Europe.

Uncinulus, Bayle. Like *Wilsonia*, but with the hinge-plate undivided, and with a well-developed cardinal process. Devonian; North America and Europe.

Hypothyris, King. Sub-cuboidal *Rhynchonellae* with a very rudimentary dorsal median septum. Plications as in *Wilsonia*. Vascular sinus frequently strongly impressed in the ventral valve. Devonian; North America and Europe.

Pugnax, Hall and Clarke. *Rhynchonellae* with a deep dorsal and shallow ventral valve, and very prominent fold and sinus; otherwise resembling *Hypothyris*. Devonian to Carboniferous; North America and Europe.

Eatonia, Hall. *Rhynchonellae* with large, flabellate, deeply excavated muscular scars in the ventral valve. No dental lamellae. Cardinal process large, resting upon a short median septum, and bifurcate at its summit. Devonian; North America.

Terebratuloidea, Waagen. *Rhynchonellae* with very large apical foramen, but without dental plates, cardinal process, or median septa. Carboniferous to Permian; India.

Rhynchopora, King (*Rhynchoporina*, Oehlert). Plicate *Rhynchonellae* with the shell substance punctate. Carboniferous to Permian; Europe and North America.

Rhynchonella, Fischer (as restricted by Hall and Clarke), (Fig. 543, *A*). Sub-pyramidal shells with a prominent anterior lingniform extension. Dental lamellae and a dorsal median septum present. No cardinal process. Jurassic and Cretaceous.

Upwards of 600 species of *Rhynchonella* have been described, most of which are found in Mesozoic strata (Figs. 543, *B*, 544). It is probable that but few of these agree with the type species, *R. loxia*, from the Upper Jura of Russia. Hall and Clarke have shown that many American Palaeozoic species belong to other genera; and Bittner has also removed from *Rhynchonella* many Triassic species. It is probable that no Palaeozoic *Rhynchonellae* s.s. exist.

Halorella, Bittner. Sharply plicated *Rhynchonellae* with a median sinus on both valves. Alpine Trias.

Austriella, Bittner. Small triangular, usually smooth-shelled *Rhynchonellae* without prominent fold and sinus. Alpine Trias.

Norella, Bittner. Like *Austriella*, but with prominent anterior fold and sinus. Alpine Trias.

Rhynchonellina, Gemellaro. Transverse *Rhynchonellae* with fine radial striae. Cardinal margin nearly straight, with a low concave ventral area.

Crura very long, ventrally curved. Median septum of dorsal valve faint. Jura; Sicily and the Alps.

Dimerella, Zittel. Small plicate shells with a high umbo and a straight hinge-line. Delthyrium large, with linear deltidial plates. Dorsal valve with a high median septum extending to the ventral valve. Alpine Trias.

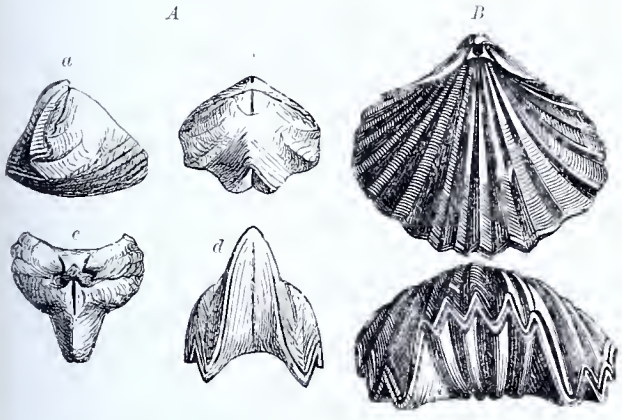


Fig. 543.

A, *Rhynchonella loxia*, Fisch. Upper Jura; Moscow. *a*, *b*, Profile and dorsal view, 1/1; *c*, Cast; *d*, Anterior view. *B*, *R. quadriplicata*, Quenst. Middle Jura; Bopfingen, Würtemberg.

Fig. 544.

A, *Rhynchonella vespertilio*, Brocchi. Upper Cretaceous; Villedieu, Touraine. 1/1. *B*, *R. lacunosa*, Schloth. sp. Upper Jura; Engelhardsberg, Franconia. Interior of dorsal valve.

Peregrinella, Oehlert. Large, strongly plicate *Rhynchonellae* without fold or sinus. Cardinal area well developed. Cretaceous; Europe.

Hemithyris, d'Orb. (Fig. 545). Smooth or faintly plicate *Rhynchonellae* with a high ventral beak and open delthyrium. No dental plates. Recent.

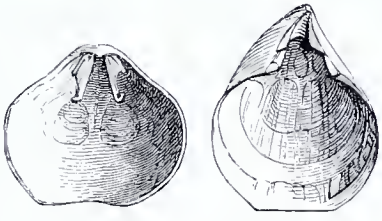


Fig. 545.

Hemithyris psittacea, Lam. sp. Recent; Mediterranean. 1/1.

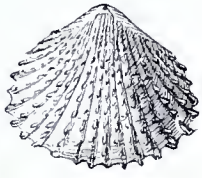


Fig. 546.

Acanthothyris spinosa, Schloth. sp. Middle Jura; Auerbach, Upper Palatinate.

Frieleia, Dall. Resembling *Hemithyris*, but with a small dorsal spondylium. Recent; American Pacific.

Acanthothyris, d'Orb. (Fig. 546). Like the last, but with well-developed dental plates, and the exterior surface covered with spines. Jura to Recent; Europe and Japanese Province.

Cryptopora, Jeffreys (*Atretia*, Jeffreys; *Neatretia*, Oehlert). Small smooth shells with an acute and prominent open ventral beak. Dental plates and a high, mesially situated, dorsal septum present. Recent.

Cyclorhina, Hall and Clarke. Devonian; North America.

Superfamily 2. TEREBRATULACEA. Waagen.

Derived Telotremata with the brachia supported by calcareous, primitive, or metamorphosed loops. Devonian to Recent.

(Section A.) Terebratula.

Terebratulacea with the loops unsupported by a median dorsal septum at any stage of growth. Brachial cirri directed outwards in larval stages.

Family 1. **Centronellidae.** Hall and Clarke.

Terebratulas with the loops developing direct and composed of two descending lamellae, uniting in the median line and forming a broad arched plate. Devonian to Triassic.

This family comprises the simplest of all Terebratuloids, and from it are probably descended the other loop-bearing families.

Centronella, Billings (Fig. 547). Commonly small, smooth, plano-convex, or concavo-convex shells, with the descending branches of the loop broadening rapidly anteriorly, and uniting in a triangular, mesially ridged plate. Devonian; North America.

Rensselaeria, Hall. Ovate or elongate-ovate striate Terebratuloids. The descending branches of the loop diverging for a short distance, thence acutely bent, converging, and uniting in an elongate triangular plate, which on the posterior margin gives off a small, posteriorly directed, rod-like process. Hinge-plate large and often much thickened. Thick dental plates present. Lower Devonian; North America and Germany.

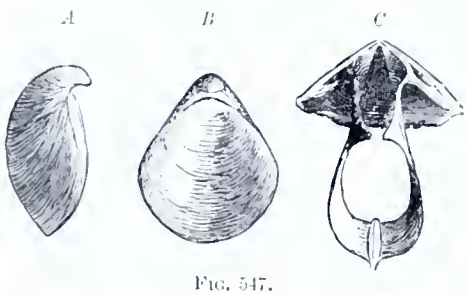


Fig. 547.

Centronella glans-fagea, Hall. Devonian; Erie County, N.Y. *A*, *B*, Profile and dorsal aspect, $^1/_1$. *C*, Loop, enlarged.

Beachia, Hall and Clarke. Lentiform finely striated *Rensselaeriae* with the lateral margins of the valves inflected, the anterior plate of the brachidium broader, and the rod-like process longer. Lower Devonian; North America.

Newberria, Hall (*Rensselandia*, Hall). Resembling *Rensselaeria* externally, but without the striate surface. Interior strongly marked by muscular scars and vascular sinuses. Devonian; North America and Europe.

Oriskania, Hall and Clarke. Large *Centronellae* with a continuous hinge-plate bearing a thin vertical spur or cardinal process. Lower Devonian; North America.

Selenella, Hall and Clarke. Biconvex Terebratuliform shells with a *Centronella*-like loop, but the triangular plate not mesially thickened. Devonian; North America.

Romingerina, Hall and Clarke. Small biconvex *Centronellae* with the median ridge on the anterior plate of the loop elevated into a high vertical lamella almost touching the ventral valve and extended both anteriorly and posteriorly. Devonian to Lower Carboniferous; North America.

Trigeria (Bayle), Hall and Clarke. Plicated, plano-convex *Centronellae*. Devonian; France, Brazil, and North America.

? *Scaphiocoelia*, Whitfield. Very large, plicate, plano- or concavo-convex, *Centronella*-like shells exteriorly. Loop unknown. Shell substance fibrous, impunctate. (?) Devonian; South America.

Juravella, Bittner. Small, smooth, biconvex shells, with a very short *Centronella*-like loop. Alpine Trias.

Nucleatula, Bittner. Like *Juravella*, but having a longer loop with a well-developed and fimbriated vertical median plate. Alpine Trias.

Dinarella, Bittner. Alpine Trias. *Chascothyris*, Holzapfel. Devonian; Germany.

Family 2. **Terebratulidae.** Gray.

Terebratulas developing originally a Centronella-like loop, and thence by a short series of metamorphoses resulting at maturity in a free loop of varying form. Devonian to Recent.

Sub-Family A. Stringocephalinae. Dall.

Terebratulidae with a long loop, following the margin of the dorsal valve, not recurved in front. Probably no median coiled arm.

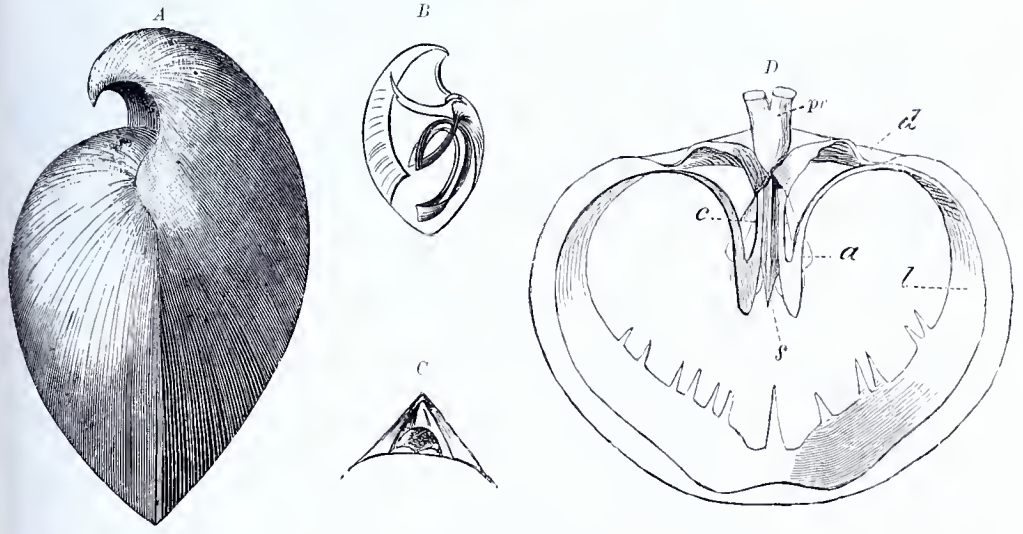


Fig. 548.

Stringocephalus Burtini, Defr. Devonian; Paffrath, near Cologne. *A*, Side-view, 2/3 natural size. *B*, Greatly reduced diagram showing brachidium and median septa. *C*, Young specimen with large delthyrium and deltidial plates. *D*, Interior of dorsal valve, natural size, partly restored (*a*, Adductors; *c*, Crura; *d*, Dental sockets; *l*, Loop; *pr*, Cardinal process; *s*, Median septum).

Stringocephalus, Defr. (Fig. 548). Devonian; Europe and North America.

Sub-Family B. Megalanterinae. Waagen.

Terebratulidae with a long loop giving off ascending branches. Devonian to Carboniferous.

Megalanteris, Oehlert (*Meganteris*, Suess). Large, smooth, equally biconvex, sub-oval shells, with the long convergent jugal processes of the loop extending beyond the connecting band of the ascending branches. Devonian; Europe and North America.

Cryptonella, Hall. Elongate oval shells with short jugal processes. Devonian to Lower Carboniferous; North America, England, and Bohemia.

Harttina, Hall and Clarke. *Centronella*-like shells with a high dorsal median septum and the descending branches of the loop laterally fringed with irregularly set spinules. Carboniferous; North America and Brazil.

? *Cryptacanthia*, White and St. John. Upper Carboniferous; North America.

Sub-Family C. TEREBRATULINAE. Dall.

Terebratulidae with a short loop. A median unpaired coiled arm exists in recent genera. Devonian to Recent.

Of this large sub-family only a few of the more important genera can be briefly considered here.

Dielasma, King (*Epithyris*, King), (Fig. 549). To the divergent crural plates is attached a shallow, often quite long, anteriorly acuminate hinge-

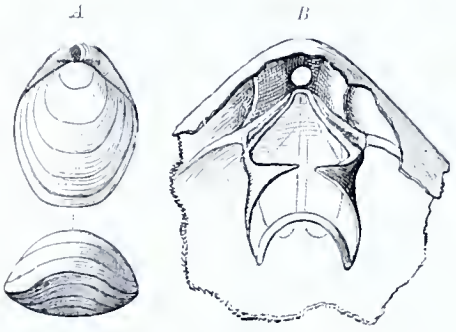


FIG. 549.

Dielasma elongata, Schloth. sp. Permian; Humbleton, England. *A*, Dorsal and anterior views, 1/1. *B*, Interior of conjoined valves, greatly enlarged (after Davidson).

FIG. 550.

Terebratulina substriata, Schloth. sp. Upper Jura; Nattheim, Würtemberg. 1/1.

FIG. 551.

Terebratula Phillipsi, Morris. Middle Jura; Egg, near Aarau, Switzerland. 1/1.

plate carrying the muscles of the dorsal valve. Devonian to Permian; Europe, India, and America.

Eunella and *Cranaena*, Hall and Clarke. Dielasmas without the adherent myiferous hinge-plate. Devonian; North America.

Beecheria, Hall and Clarke. Smooth-shelled Dielasmas without dental plates, but with the

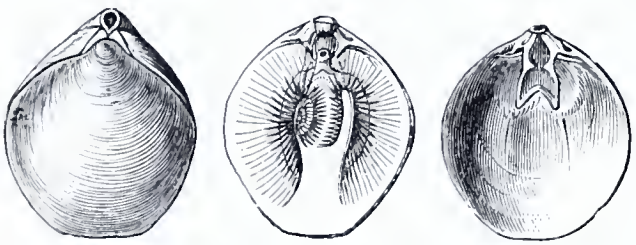


FIG. 552.

Liothyrina vitrea, Linn. sp. Recent; Mediterranean. 1/1.

FIG. 553.

Pygope diphya, Colonna. Tithonian; Trent, Tyrol. 1/1.

myiferous plate wholly attached to the dorsal valve. Carboniferous; North America and India.

Dielasmina, Waagen. Plicated Dielasmas. Carboniferous; India.

Hemiptychina, Waagen. Plicated Dielasmas without dental plates. Carboniferous to Permian; India.

Notothyris, Waagen. Carboniferous; India. *Terebratulina*, d'Orbigny (Fig. 550). Jura to Recent. Distribution general.

Terebratula, Klein, 1753 (Fig. 551). Genus not well known. Mesozoic or Tertiary.

Liothyrina, Oehlert (*Liothyris*, Douvillé), (Fig. 552). Tertiary to Recent.

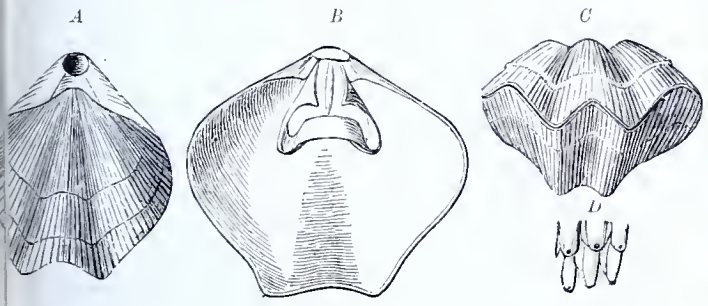


Fig. 554.

Dictyothyris coarctata, Park sp. Great Oolite; Bath, England. *A-C*, Three views of the natural size. *D*, Portion of outer surface, enlarged.

Fig. 555.

Glossothyris nucleata, Schloth. sp. Upper Jura; Engelhardsberg, Franconia. 1/1.

Pygope, Link (*Diphyites*, Schröter; *Pugites*, de Hann; *Antinomia*, Catullo), (Fig. 553). Shell originally bilobed, the two lobes often uniting anteriorly in adult specimens, but leaving posteriorly a median hollow space passing through the shell. Jura; Europe.

Dictyothyris, Douvillé (Fig. 554); *Glossothyris*, Douvillé (Fig. 555); (?) *Disculina*, Deslong. All from the European Jura.

Zugmeyeria and *Rhaetina*, Waagen; and *Propygope*, Bittner. Trias; Europe.

Sub-Family D. Discoliinae. Beecher.

Terebratulidae with the loop short and no coiled median arm. (?) Cretaceous, Recent.

Discolia and *Eucalathis*, Fischer and Oehlert. Recent.

? *Agulhasia*, King. Small *Terebratulina*-like shells with the ventral beak greatly elevated and a triangular false cardinal area. Cretaceous to Recent.

(Section B.) Terebratella.

Terebratulacea with the loop supported by a median dorsal septum throughout life, or only in the younger stages. Brachial cirri directed inwards during larval stages. This section has two phyla having a common origin, now geographically separated in two provinces, one austral, the other boreal.

Family 1. **Terebratellidae.** King (emend. Beecher).

Terebratulacea with the loop in the higher genera composed of two primary and two secondary lamellae, passing through a series of distinct metamorphoses while attached to a dorsal septum. Devonian to Recent.

Sub-Family A. Tropidoleptinae. Schuchert.

Terebratellidae with the loop consisting of two slender descending branches, uniting with a high, vertical septum. Devonian.

Tropidoleptus, Hall. Plano-convex plicated shells with a long straight and narrow cardinal area. Teeth and dental sockets corrugated on their outer surfaces. Devonian; America, Europe, and South Africa.

Sub-Family B. Megathyrinae. Dall (emend. Beecher).

Terebratellidae in which the loop is composed of descending branches only, passing in the highest genus through stages correlative with Gwynia, Cistella, and Megathyris. The lower genera do not complete the series. The original stock for the two following sub-families. Jurassic to Recent.

Gwynia, King. Minute, elongate-oval, smooth shells with a short, nearly straight hinge-line. Neither septa nor loop. Brachia primitive, consisting of a circlet of cirri. Recent.

Fig. 556.

Cistella bilocularis, Desl. sp. Cenomanian; La Manche. 1/1.

Fig. 557.

Megathyris decollata, Chem. sp. Recent; Mediterranean. Interior of dorsal valve, 4/1 (after Davidson).

Zellania, Moore. Minute shells without a loop, but with a median septum in each valve. Lias; Europe.

Cistella, Gray (Fig. 556). Externally like *Megathyris*, but without lateral septa. Cretaceous to Recent; Europe.

Megathyris, d'Orbigny (*Argiope*, Deslong.), (Fig. 557). Transversely elongate, plicate, shells with long and straight hinge-line. Dorsal valve with three or five septa, causing the brachidium to have four lobes. Jura to Recent; Europe.

Sub-Family C. Dallininae. Beecher.

Terebratellidae with the loop composed of descending and ascending lamellae, passing in the highest genera through metamorphoses comparable to the adult structure of Platidia, Ismenia, Muehlfeldtia, Terebratalia, and Dallina. The lower genera, therefore, do not progress to the final stages. Jura to Recent. Recent genera restricted to boreal seas.

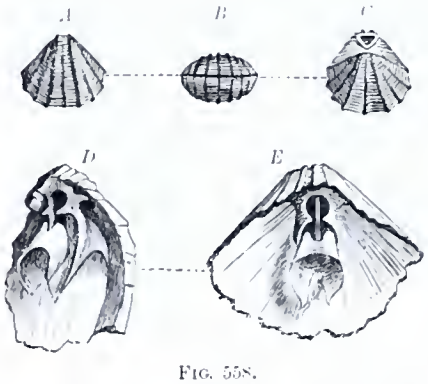


Fig. 558.

Muehlfeldtia pectunculus, Schloth. sp. Upper Jura; Engelhardsberg, Franconia. *A-C*, Shell of the natural size. *D*, *E*, Two views of loop, enlarged.

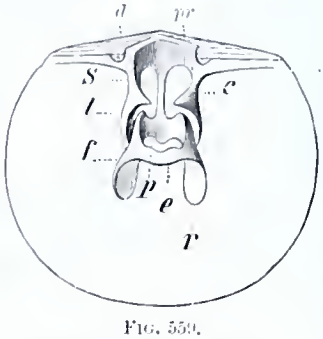


Fig. 559.

Muehlfeldtia truncata, Gemm. sp. Recent; Mediterranean. Interior of dorsal valve (*c*, Crura; *d*, Dental sockets; *e*, Jugum; *f*, *l*, Ascending and descending branches of loop; *p*, Process attached to median septum; *pr*, Cardinal process; *S*, Median septum).

Platidia, Costa (*Morrisia*, Davidson). Small, smooth, biconvex shells with

a large pedicle opening common to both valves. In the dorsal valve there is a high vertical plate to which are attached the descending branches; ascending branches not represented. Recent.

Ismenia, King. Coarsely plicate shells with the loop consisting of fimbriate descending branches and simple ascending branches. Jura.

Muehlfeldtia, Bayle (*Megerlea*, King), (Figs. 558, 559). Jura to Recent.

Frenulina, Dall. Sub-genus of *Muehlfeldtia*. Recent.

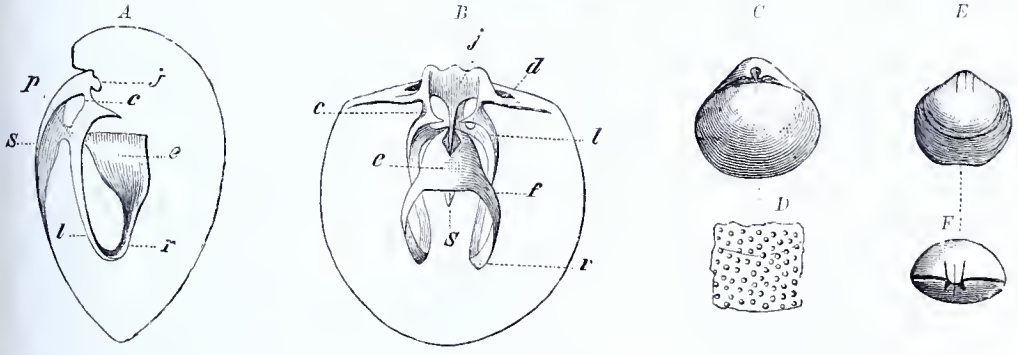


FIG. 560.

A, *B*, *Kingena lima*, Defr. Cretaceous; England. Lateral and frontal aspect of loop, enlarged (after Davidson). *C*, Specimen from the Galeritenpläner of Salzgitter, 1/1. *D*, External surface, enlarged. *E*, *F*, *Kingena Friesensis*, Schrüfer sp. Upper Jura; Gruibingen, Würtemberg. 1/1. (*c*, Crura; *d*, Dental sockets; *e*, Jugum; *f*, *l*, Ascending and descending branches of loop; *j*, Cardinal process; *r*, Point of recurvature of loop; *S*, Median septum).

Terebratalia, Beecher. Shell when adult like *Terebratella*, but passing through a quite different series of metamorphoses. Recent.

Dallina, Beecher. Elongate *Terebrataliae* with a small cardinal process and a ventral median sinus. Tertiary to Recent.

Macandrevia, King. Elongate *Terebrataliae* with dental plates and no cardinal process. Recent. A sub-genus of *Eudesia*, according to Dall.

Laqueus, Dall (*Frenula*, Dall). Like *Terebratalia*, but the loop has two lateral processes connecting the ascending and descending branches. Recent.

Kingena, Davidson (*Kingia*, Schoenbach), (Fig. 560). Cretaceous; Europe and North America.

Lyra, Cumberland (*Terebrirostra*, d'Orbigny), (Fig. 561). Cretaceous; Europe.

FIG. 561.

Lyra Neocomiensis, d'Orb. Lower Cretaceous; Morteau, Doubs. Natural size.

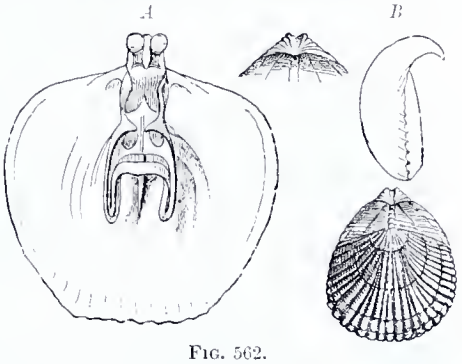


FIG. 562.

A, *Trigonosemus elegans*, Defr. White Chalk; England. Interior of dorsal valve, enlarged (after Davidson). *B*, *T. Palissyi*, Woodw. Upper Cretaceous; Ciply, Belgium. 1/1. (Drawn from nature.)

Trigonosemus, Koenig (*Fissurirostra*, *Fissirostra*, d'Orb.; *Delthyridea*, King), (Fig. 562). Cretaceous; Europe.

Microthyris, Deslongchamps (*Ornithella*, Deslong.), (Fig. 563). Jura. *Zeilleria*, Bayle, seems to differ only in having a biplicate dorsal valve. Europe.

Aulacothyris, Douvillé (Fig. 564). Trias to Cretaceous; Europe. *Eudesia*,

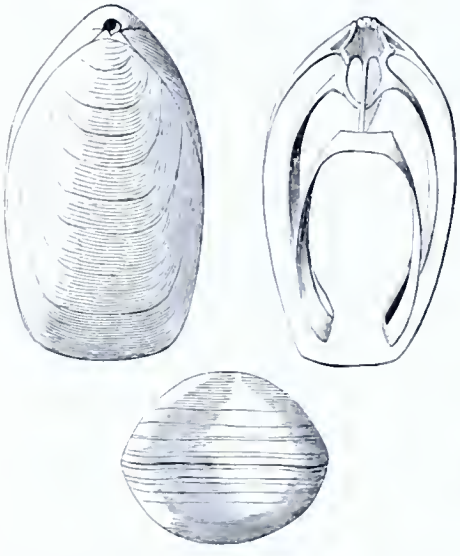


Fig. 563

Microthyris lagenalis, Schloth. sp. Cornbrash; Rushden, England. 1/1 (after Davidson).

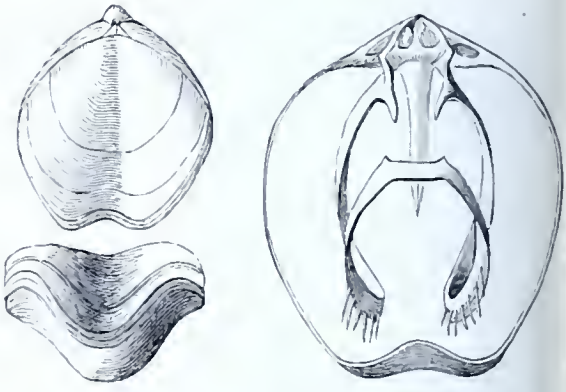


Fig. 564.

Aulacothyris resupinata, Sow. sp. Middle Lias; Ilminster, England (after Deslongchamps).

King (*Orthotoma*, *Trigonella*, Quenstedt; *Flabellothyris*, Deslong.) Jura; Europe.

Fimbriothyris and *Epicyrta*, Deslong. Jura. *Camerothyris*, Bittner. Trias. *Cincta*, Quenstedt. Jura. *Antiptychina*, Zittel. Jura. *Plesiothyris*, Douvillé. Jura; Europe.

? *Hunniphoria*, Suess; ? *Cruratula*, Bittner; ? *Orthoidea*, Friren.

Sub-Family D. Magellaninae. Beecher.

Terebratellidae with the loop composed of descending and ascending branches, passing

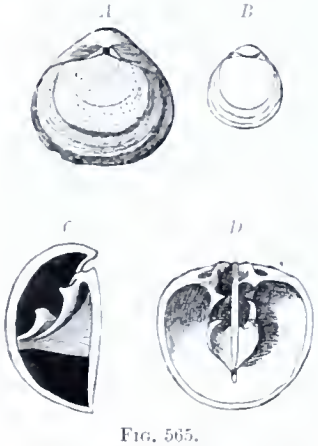


Fig. 565.

Magas pumilus, Sow. White Chalk; Mendon, near Paris. *A*, *B*, Shell. 1/1. *C*. Vertical section. *D*. Interior of dorsal valve.

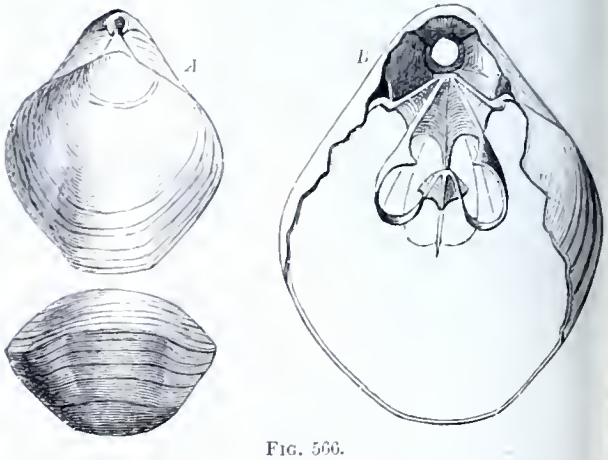


Fig. 566.

Coenothyris vulgaris, Schloth. sp. Muschelkalk; Würzburg. *A*, Dorsal and anterior views, 1/1. *B*. Loop enlarged and restored from sections treated with acid (partly after Koschinsky).

in the higher genera through metamorphoses comparable to the adult structure of Bou-

chardia, Magas, Magasella, Terebratella, and Magellania. The lower genera become adult before reaching the terminal stages. Jura to Recent. Recent genera restricted to austral seas.

Bouchardia, Davidson (*Pachyrhynchus*, King). Recent; South Atlantic.

Magas, Sowerby (Fig. 565). Cretaceous; Europe. *Magasella*, Dall. Recent. *Coenothyris*, Douvillé (Fig. 566). Trias.

Terebratella, d'Orbigny (*Delthyris*, Menke; *Ismenia*, King; *Waltonia*, Davidson), (Fig. 567). Jura to Recent.

Magellania, Bayle (*Waldheimia*, King; *Neothyris*, Douvillé), (Fig. 568, also Figs. 497, 498). Jura to Recent.

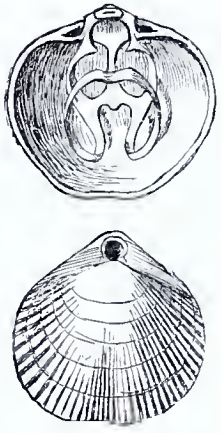


Fig. 567.

Terebratella dorsata, Lam. sp. Recent; Chili. 1/1.

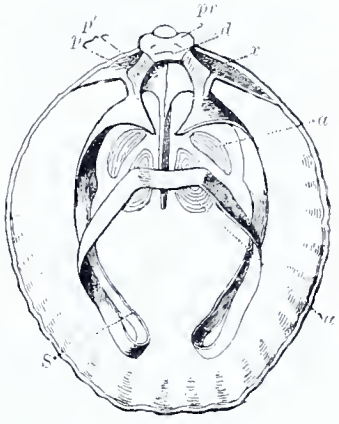


Fig. 568.

Magellania flavescens, Val. Recent; Australia. Interior of dorsal valve, somewhat enlarged.

Rhynchorina, Oehlert. Cretaceous. *Megerlina*, Deslongchamps. Recent. *Kraussina*, Davidson (*Kraussia*, Davidson). Recent. *Mannia*, Dewalque. Miocene. ? *Rhynchora*, Dalman. Cretaceous.

Superfamily 3. SPIRIFERACEA. Waagen.

Telotremata with the adult brachia supported by calcareous spiral lamellae or spiralia. Ordovician to Jurassic.

The *Spiriferacea* are abundantly represented from the Silurian to the Carboniferous, during which time the jugum undergoes many and often rapid changes. The brachidia in *Zygospira* are known to begin with a *Centronella*-like loop, as in the primitive *Terebratulacea*.

Family 1. Atrypidae. Gill.

Spiriferacea with the crura directly continuous with the primary lamellae, which diverge widely and have the spiral cones between them. Jugum simple, complete, or incomplete. Ordovician to Devonian.

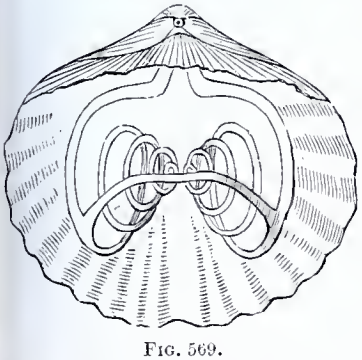


Fig. 569.

Zygospira modesta, Hall. Ordovician; Cincinnati, Ohio. 3/1 (after Hall).

This family is divided into *Zygospirinae*, *Dayinae*, and *Atrypinae*, according to modifications of the jugum or position of the spirals.

Zygospira, Hall (*Anazyga*, Davidson; *Orthonomaea*, Hall; *Hallina*, Winchell and Schuchert; *Protozyga*, Hall and Clarke (Fig. 569). Like *Atrypa*, but small, and the spirals composed of fewer coils. Jugum a simple connecting band, situated rather anteriorly. Surface sharply plicate, never lamellose. Ordovician and Silurian; North America.

Catazyga, Hall and Clarke. More rotund and finely striated than *Zygospira*.

with the complete jugum decidedly posterior in position. Ordovician and Silurian; North America.

Atrypina, Hall and Clarke. Primitive *Atrypae* with few plications, and but three or four volutions in each spiral. Jugum as in *Atrypa*, but continuous. Silurian to Devonian; North America and Europe.

Fig. 570.

Glassia obovata, Sow. sp. Silurian; Wenlock, England. Interior of dorsal valve, $^3/_1$ (after Davidson).

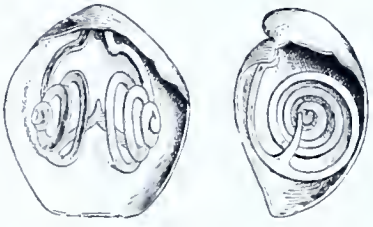


Fig. 571.

Dayia navicula, Sow. sp. Silurian; Ludlow, Shropshire. $^5/_2$ (after Davidson).

Glassia, Davidson (Fig. 570). Small smooth shells, with the apices of the laterally compressed spirals situated at the centre of the brachial cavity. Jugum similar to that of *Atrypina*. Ordovician to Devonian; Europe.

Dayia, Davidson (Fig. 571). Small smooth shells, with the jugum situated anteriorly, and drawn out posteriorly into a simple short process. Spiralia laterally directed. Silurian; Europe.

Atrypa, Dalman (*Cleiothyris*, Phill.; *Spirigerina*, d'Orb.), (Fig. 572). Shell radially plicated, usually with lamellar expansions or hollow spines. Spirals introverted, dorso-medially directed. Jugum extremely posterior in position,

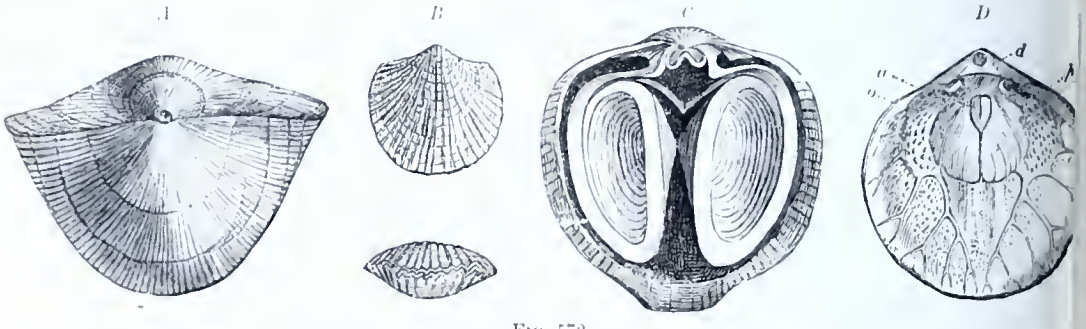


Fig. 572.

Atrypa reticularis, Lin. sp. Middle Devonian; Gerolstein, Eifel. *A*, Dorsal aspect of adult specimen. *B*, Ventral aspect and profile of young shell. *C*, Interior of dorsal valve, showing spiralia, crura, and jugum. *D*, Ventral valve, showing muscular and vascular impressions (*a*, Adductors; *c*, Diductors; *d*, Deltidial plates; *o*, Ovaries; *p*, Pedicle muscle).

and complete in young stages; but mesially absorbed at maturity. Widely distributed in the Silurian and Devonian.

Gruenewaldtia, Tschernyschew. *Atrypa*-like shells, but with the relative convexity of the valves reversed. Devonian; Russia.

? *Karpinskya*, Tschernyschew. Elongate, *Atrypa*-like shells, with a median dorsal septum. Devonian; Russia.

? *Clintonella*, Hall and Clarke. Silurian; North America.

Family 2. Spiriferidae. King.

Spiriferacea with the crura directly continuous with the bases of the primary lamellae, which are situated between the laterally directed spiralia. Jugum simple, complete, or incomplete. Silurian to Jurassic.

This family is divided into the following sub-families—*Suessiinae*, *Uncitinae*, and *Trigonotretinae*.

Cyrtina, Davidson (Fig. 573). *Cyrtia*-like shells, with the dental lamellae converging and united with the median septum. Loop V-shaped, complete. Silurian to Lower Carboniferous. Distribution general.

Thecocyrtella, Bittner. Very small, ventrally cemented, smooth-shelled *Cyrtinae*. Alpine Trias.

Bittnerula, Hall and Clarke. Like *Thecocyrtella*, but with the abbreviated

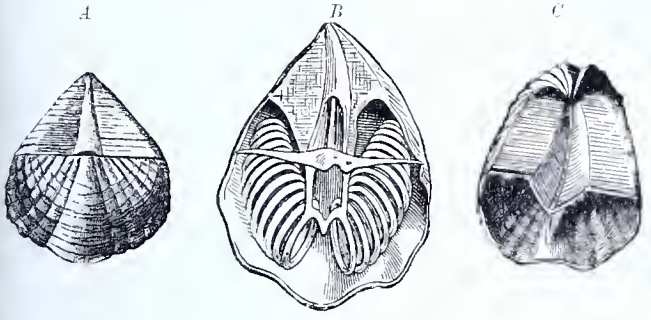


Fig. 573

A, *Cyrtina heteroclyta*, Defr. sp. Devonian; Eitel. 1/1. *B*, Shell with dorsal valve mostly removed, showing spiralia, 3/2 (after Davidson). *C*, *Cyrtina carbonaria*, M'Coy. Carboniferous Limestone; Kendal, Ireland. 1/1. Interior of ventral valve. The pseudodeltidium is removed to show the dental plates and median septum.

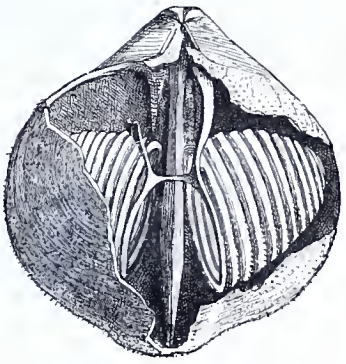


Fig. 574.

Spiriferina rostrata, Sow. sp. Middle Lias; Ilminster. 1/1 (after Davidson).

dental plates uniting with the very high median septum, forming a transverse platform beneath the united deltidial plates. Alpine Trias.

Spiriferina, d'Orb. (Fig. 574). Like *Spirifer*, but with the shell substance punctate, and a prominent ventral median septum. Loop simple, complete. Carboniferous to Jura.

Suessia, Deslongchamps. Similar to *Spiriferina*, but the dental plates not extending to the bottom of the valve. Jugum with a median process. Jura; Europe.

Uncites, Defrance (Fig. 575). Shells rostrate, striate, with the ventral beak long, frequently distorted and arched. No cardinal area. Deltidial plates united, forming a concave plate. Pouch-like plates just within the margins of the dorsal valve. Devonian; Germany.

Uncinella, Waagen. Carboniferous; India.

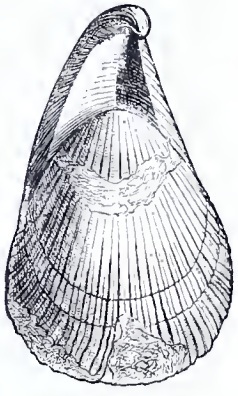


Fig. 575.

Uncites gryphus, Schloth. Devonian; Benzberg, near Cologne. 1/1.

Spirifer, Sowerby (*Trigonotreta*, Koenig; *Choristites*, Fischer de Waldheim; *Brachythyris* and *Fusella*, M'Coy; *Hysterolithus*, Quenstedt), (Fig. 576). Shell radially plicated or striated, crossed by concentric growth-lines, lamellae, simple, or compound spines. Hinge-line generally long and straight. Ventral valve usually with moderately high cardinal area, and stout simple teeth supported by short dental lamellae. Delthyrium open. Spirals directed towards the cardinal angles of the valves. Jugum at maturity represented by two short spur-like processes, which are not in contact with each other. Generally distributed and extraordinarily abundant in the Silurian, Devonian, and Carboniferous.

The species of *Spirifer* have recently been grouped by Hall and Clarke into six sections as follows:—*Radiati*, with fine filiform striae; *Lamellosi*, with concentric

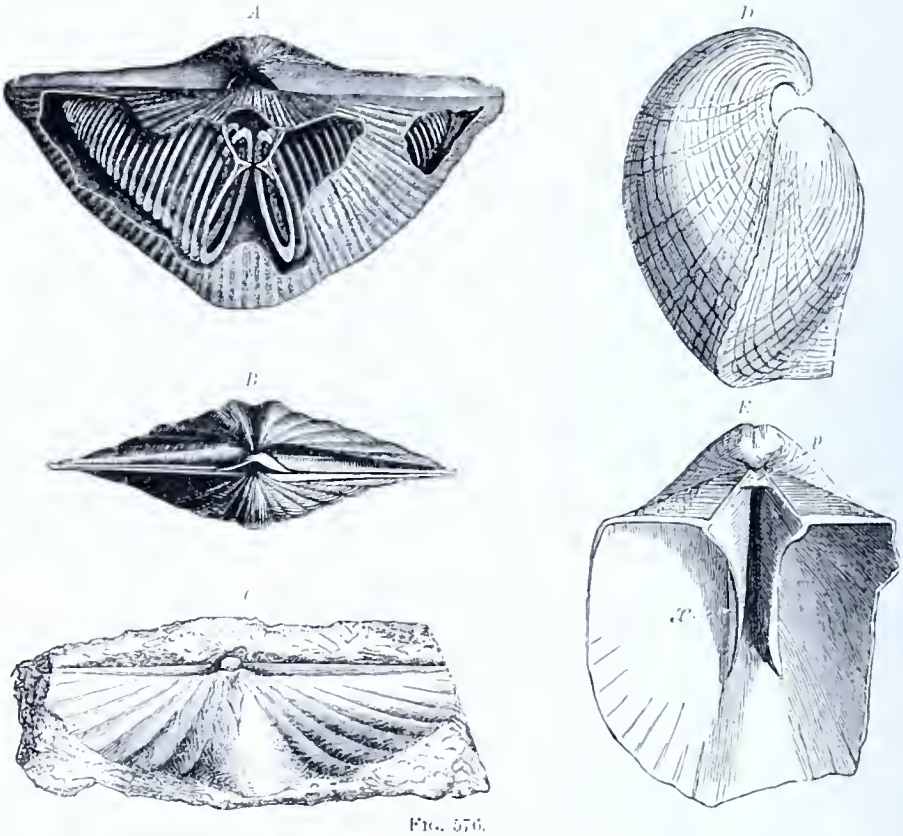


Fig. 576.

A, *Spirifer striatus*, Sow. Carboniferous Limestone; Ireland. Portion of dorsal valve removed, showing spiralia, $^3/_4$ (after Davidson). *B*, *S. speciosus*, Schloth. sp. Devonian: Eifel. $^1/_1$. *C*, *S. macropterus*, Goldf. sp. Devonian; Coblenz. Cast, $^1/_1$. *D*, *S. Mosquensis*, Vern. Sub-Carboniferous; Moscow. *E*, Same, interior of ventral valve, $^1/_1$ (*p*, Pseudodeltidium; *x*, Dental plates).

lamellae (= *Delthyris*, Dalman); *Fimbriati*, with concentric rows of fine spines (= *Reticularia*, M'Coy); *Aperturati*, with plications on fold and sinus; *Ostiolati*, with the median fold and sinus without plications; *Glabrati*, with the surface smooth and glabrous (= *Martinia*, M'Coy; *Martiniopsis*, Waagen; and *Mentzelia*, Quenstedt).

Cyrtia, Dalman (Fig. 577). Distinguished from *Spirifer* by having an unusually high ventral area, with its delthyrium closed by a perforated deltarium. Silurian to Devonian; Europe and North America.

Fig. 577.

Cyrtia exporrecta, Dalm. Silurian; Gottland. Natural size.

Syringothyris, Winchell. *Spirifer*-like shells, usually with large and erect cardinal areas and an internal tube or syrinx, situated in the delthyrium. Carboniferous; North America and Europe.

Ambocoelia, Hall. Small, concave, or plano-convex, usually smooth *Spirifer*-like shells. Four well-defined adductor scars near the anterior margin in the dorsal shell. Devonian to Carboniferous; North America and Europe.

Verneuilia, Hall and Clarke. Small Spirifers, with a deep median sinus and two pronounced divergent ridges on each valve. Devonian to Carboniferous; Europe.

Metaplasia, Hall and Clarke. *Spirifer*-like shells, with a median fold on the ventral valve and a sinus on the dorsal valve. Lower Devonian; North America.

Family 3. **Athyridae.** Phillips.

Spiriferacea with the bases of the primary lamellae situated between the spiralia, and sharply recurved dorsally at their junction with the crura. Spiralia more or less laterally directed. Jugum complete, V-shaped, with the apex drawn out into a simple, bifurcated, or otherwise modified process. Silurian to Trias.

This large, chiefly Palaeozoic family, with its numerous highly differentiated species, is divided into six sub-families, on the basis of the simplicity or complexity of the jugum. These are the *Rhynchospirinae*, *Hindellinae*, *Athyrinae*, *Diplospirinae*, *Koninckininae*, and *Meristellinae*.

Rhynchospira, Hall (Fig. 578, *C*, *D*). Rostrate, radially plicate shells with a short curved hinge-line; apex truncated by a circular pedicle opening. Dorsal hinge-plate like that of *Trematospira*. Spirals with from six to nine volutions. Jugum V-shaped, expanding apically and terminating posteriorly in an oblique edge. Shell structure punctate. Devonian to Lower Carboniferous; North America and Europe.

Homoeospira, Hall and Clarke. Like the last, but differs in having a linear cardinal process separating the crural plates. Jugum not apically expanded, but terminating in an acute stem. Silurian; North America.

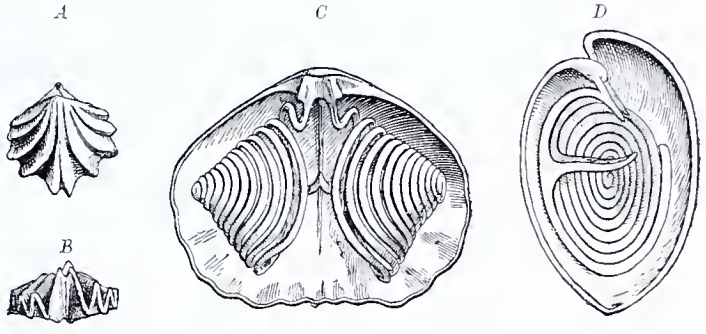


Fig. 578.

A, *B*, *Ptychospira ferita*, von Buch. Devonian; Gerolstein, Eifel. 1/1. *C*, *D*, *Rhynchospira Salteri*, David. Silurian; Wenlock, Shropshire. *C*, Interior of dorsal valve. *D*, Median vertical section through both valves, 3/1 (after Davidson).

Ptychospira, Hall and Clarke (Fig. 578, *A*, *B*). Like *Rhynchospira*, but with a few angular plications. The jugum has a long simple process passing outward between the coils to near the inner surface of the ventral valve. Devonian to Lower Carboniferous; North America and Germany.

Retzia, King (*Trigeria*, Bayle). Resembling *Rhynchospira* externally. The ventral umbonal cavity has a split tube. The single process of the jugum terminally forked. Devonian; Europe.

This genus formerly contained all shells having a Retzioid exterior. At present, however, but a single species is admitted.

Hustedia, Hall and Clarke. Externally like *Eumetria*, but with coarse plications, and internally with a split tube, as in *Retzia*. Spirals and jugum similar to that of *Eumetria*, but with fimbria and spinules respectively. Upper Carboniferous; America, Europe, India, and China.

Trematospira, Hall. Transverse *Rhynchospirae*. Silurian and Devonian; North America.

Parazyga, Hall and Clarke (Fig. 579). Like *Trematospira*, but with the fine, simple ribs covered with very delicate, short, hair-like spines. Devonian; North America.

Eumetria, Hall. Elongate terebratuliform shells with numerous fine radiating striae. Hinge-line short. Dorsal hinge-plate very complicated. Jugum similar to that of *Retzia*, but the terminally bifurcated process is extended backward at an abrupt angle, and terminates just in front of the apices of the primary lamellae. Shell structure punctate. Lower Carboniferous; North America and Europe.

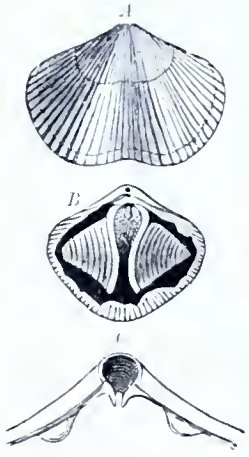


Fig. 579.

Parazyga hirsuta, Hall. Devonian; Lonisville, Kentucky. *A*, Shell of the natural size. *B*, Same with dorsal valve partly broken open, showing spiralia. *C*, Hinge-line of ventral valve, enlarged (after Hall).

Acambona, White. Carboniferous; North America.

Hindella, Davidson (? *Whitfieldella*, Hall and Clarke). Ovate or elongate, sub-equally convex, smooth, Athyroid shells. The V-shaped jugum has a short, acute process. A dorsal median septum present. Silurian and Devonian; North America.

Hyattella, H. and C. Similar to *Whitfieldella*, but compactly sub-pentahedral, and without the dorsal median septum. Silurian; North America.

Nucleospira, Hall (Fig. 580). Sub-circular, biconvex shells with numerous, fine, short spinules. Jugum with a long, straight, simple process. Silurian to Lower Carboniferous; North America and Europe.

Anoplotheca, Sandberger (*Bifida*, Davidson). Concavo-convex small shells with few plications, crossed by fine, often imbricating growth lines. Jugum originating near the mid-length of the primary lamellae, uniting and forming a simple upright stem articulating in a cavity in the ventral valve. Dorsal valve with a high median septum. Devonian: Germany and France.

Coelospira, Hall (*Leptocoelia*, Hall). Shells externally much like *Atrypa*, but with laterally directed spirals. Jugum similar to that of *Anoplotheca*. Silurian and Devonian; America, Europe, and South Africa.

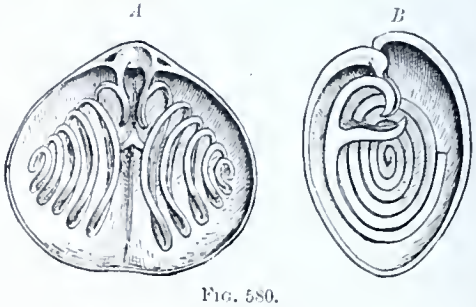


Fig. 580.

Nucleospira pisum, Sow. Silurian; Wenlock, England. *A*, Interior of dorsal valve. *B*, Vertical section through both valves, 5/2 (after Davidson).

Anabia, Clarke. Similar to *Coelospira*, but with a highly convex dorsal valve. Silurian; Brazil.

Vitulina, Hall. Like *Coelospira*, but with few plications and a long hinge-line. Plications covered with fine radiating lines or rows of pustules. Devonian; America and South Africa.

Meristina (*Whitfieldia*, Davidson), (Fig. 581). Biconvex, smooth-shelled Athyroids. Jugal stem with a short bifurcation. Silurian; North America and Europe.

Glassina, Hall and Clarke. Like *Meristina*, but with the bifurcations of the jugum originating directly from its apex. Silurian; England.

Athyris, M'Coy (*Spirigera*, d'Orbigny; *Euthyris*, Quenstedt), (Fig. 582).

Sub-equally biconvex shells with concentric growth lines extended into lamellae. Ventral umbo not prominent, incurved, usually concealing the

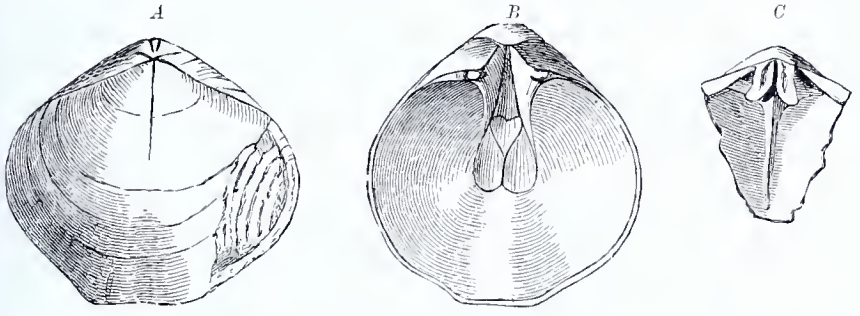


FIG. 581.

Meristina tumida, Dalm. sp. Silurian; Gottland. *A*, Shell of the natural size. *B*, Interior of ventral valve. *C*, Hinge-line and median septum of dorsal valve.

pedicle opening and deltidial plates. Teeth supported by dental lamellae. Hinge-plate of the dorsal valve perforated by a "visceral foramen." The

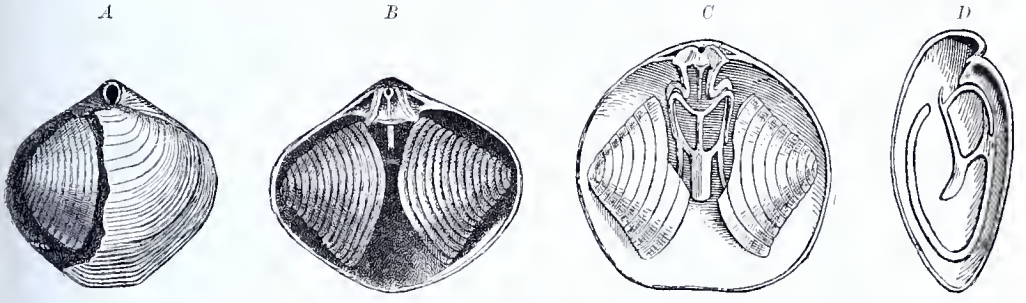


FIG. 582.

Athyris concentrica, von Buch sp. *A*, Shell with dorsal valve partly removed. *B*, Interior of dorsal valve, 1/1. *C*, *D*, Frontal and lateral aspect of spiralia (after Davidson).

peculiar jugum of this genus is illustrated in Fig. 582, *C*, *D*. Devonian and Carboniferous. Distribution general.

Actinoconchus, M'Coy. Athyroids with very wide radially striate concentric lamellae. Carboniferous; Europe.

Cleiothyris, King. Athyroids with concentric rows of flat spinules. Carboniferous and Permian. Distribution general.

Seminula, M'Coy. Smooth-shelled Athyroids. Dorsal hinge-plate very prominent. Carboniferous. Distribution general.

Spirigerella, Waagen. Carboniferous; South America and India.

Amphitomella, Bittner. Smooth-shelled Athyroids with a double cardinal process and median septa in each valve. Alpine Trias.

FIG. 583.

Tetractinella trigonella, Schloth. sp. Muschelkalk; Recoaro, Italy. 1/1.

Tetractinella, Bittner (*Plicigera*, Bittner), (Fig. 583). Athyroids with four corresponding ribs on each valve. Alpine Trias.

Pentactinella, Bittner. Athyroids with five corresponding ribs on each valve. Alpine Trias.

Anomactinella, Bittner. Athyroids with a number of angular alternating ribs towards the anterior margins. Alpine Trias.

Pomatospirella, Bittner. Small smooth shells having the contour of *Dayia* or *Cyclospira*. Alpine Trias.

Kayseria, Davidson. Lenticular, plicated shells with a median plicated sinus on both valves. Jugum with a ventral articulating process and the bifurcations continued between the spiral ribbons to their outer ends. Devonian; Germany.

Diplospirella, Bittner. Athyroids with the jugal processes coextensive with the principal spiral coils. Alpine Trias.

Pexidella, Bittner. Athyroids differing from *Diplospirella* in that the jugum is much reduced and situated in the umbonal region. Valves much thickened in the apical region. Alpine Trias.

Euractinella, Bittner. Diplospirelloids with short corresponding ribs. Alpine Trias.

Anisactinella, Bittner. Diplospirelloids with alternating ribs. The secondary spiral coils give off a process which returns and joins the jugum. Alpine Trias.

Koninckina, Suess (Fig. 584). Shell sub-orbicular, concavo-convex, smooth, with a straight hinge-line, or Strophomenoid in external appearance. Car-

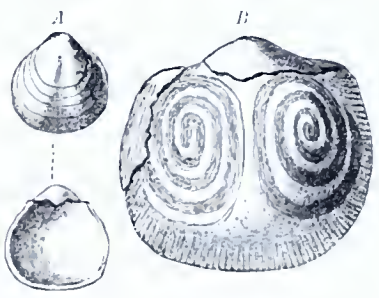


Fig. 584.

Koninckina Leonhardi, Wissm. sp. Upper Trias; St. Cassian, Tyrol. *A*, Shell showing spiralia, enlarged. *B*, Ventral and dorsal aspects, $^1/_1$.

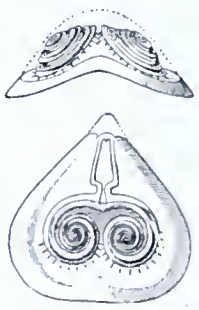


Fig. 585.

Amphiclina, with restored brachidia (after Bittner).

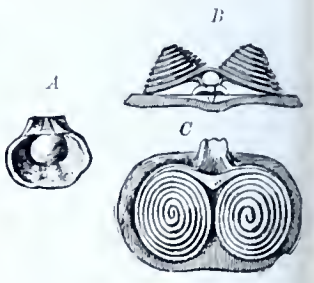


Fig. 586.

Thecospira Haidingeri, Suess sp. Rhaetic; Starhemberg, Austria. *A*, Ventral valve, $^1/_1$. *B*, *C*, Brachidia, enlarged (after Zugmeyer).

dinal area obsolete at maturity. The accessory spirals take their origin from the upper surface of the jugum, and are coextensive with the primary spirals. Trias; Europe.

Amphiclina, Laube (Fig. 585). Like *Koninckina*, but sub-trigonal in outline, and with well-developed cardinal area and deltidial plates. Trias and Jura; Europe.

Koninckella, Munier-Chalmas. Similar to *Amphiclina*, but with well-developed cardinal process. Trias and Jura; Europe.

Amphiclinodonta, Bittner. Like *Amphiclina*, but with interlocking denticulate ridges and tubercles within the margins of the valves. Alpine Trias.

Koninckodonta, Bittner. Like *Koninckina*, but with prominent cardinal areas and a row of sub-marginal thickened tubercles on the interior of the ventral valve, which interlock with similar callosities on the dorsal valve. Alpine Trias.

Thecospira, Zugmayer (Fig. 586). Ventrally cemented *Koninckinae* with well-developed cardinal area and cardinal process. Alpine Trias.

Meristella, Hall. Externally like *Merista*, but without spondylia. Apex of jugum with two annular processes. Devonian; North and South America and Europe.

Charionella, Billings. Similar to the last, but with a greatly modified hinge-plate. Devonian; North America.

Pentagonia, Cozzens (*Goniocoelia*, Hall). *Meristellae* with a broad, angular, sharply limited, ventral sinus and abrupt lateral slopes. Dorsal valve with

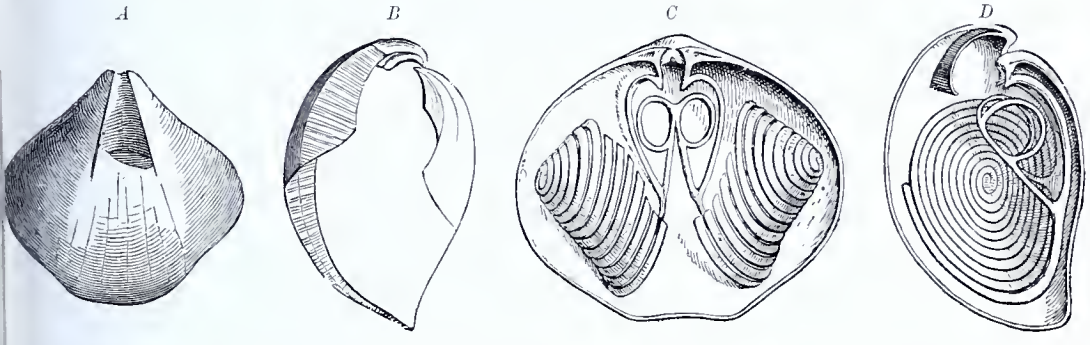


FIG. 587.

Merista herculea, Barr. sp. Devonian (F^2); Konieprus, Bohemia. *A*, External aspect of ventral valve, broken away near the apex so as to show the "shoe-lifter process," 1/1. *B*, Fractured shell showing median septum; spiralia destroyed (after Barrande). *C*, *D*, Frontal and lateral views of spiralia, slightly enlarged (after Davidson).

a wide, rounded fold, divided by a narrow sinus and umbo-laterally with two short flanges. Devonian; North America.

Merista, Suess (*Camarium*, Hall), (Fig. 587). Like *Meristella*, but with a spondylium. Silurian and Devonian; Europe and North America.

Dicamara, Hall and Clarke. *Meristellae* with a spondylium ("shoe-lifter process") and brachidium. Europe.

Dioristella, Bittner. Similar to *Meristella*. Alpine Trias.

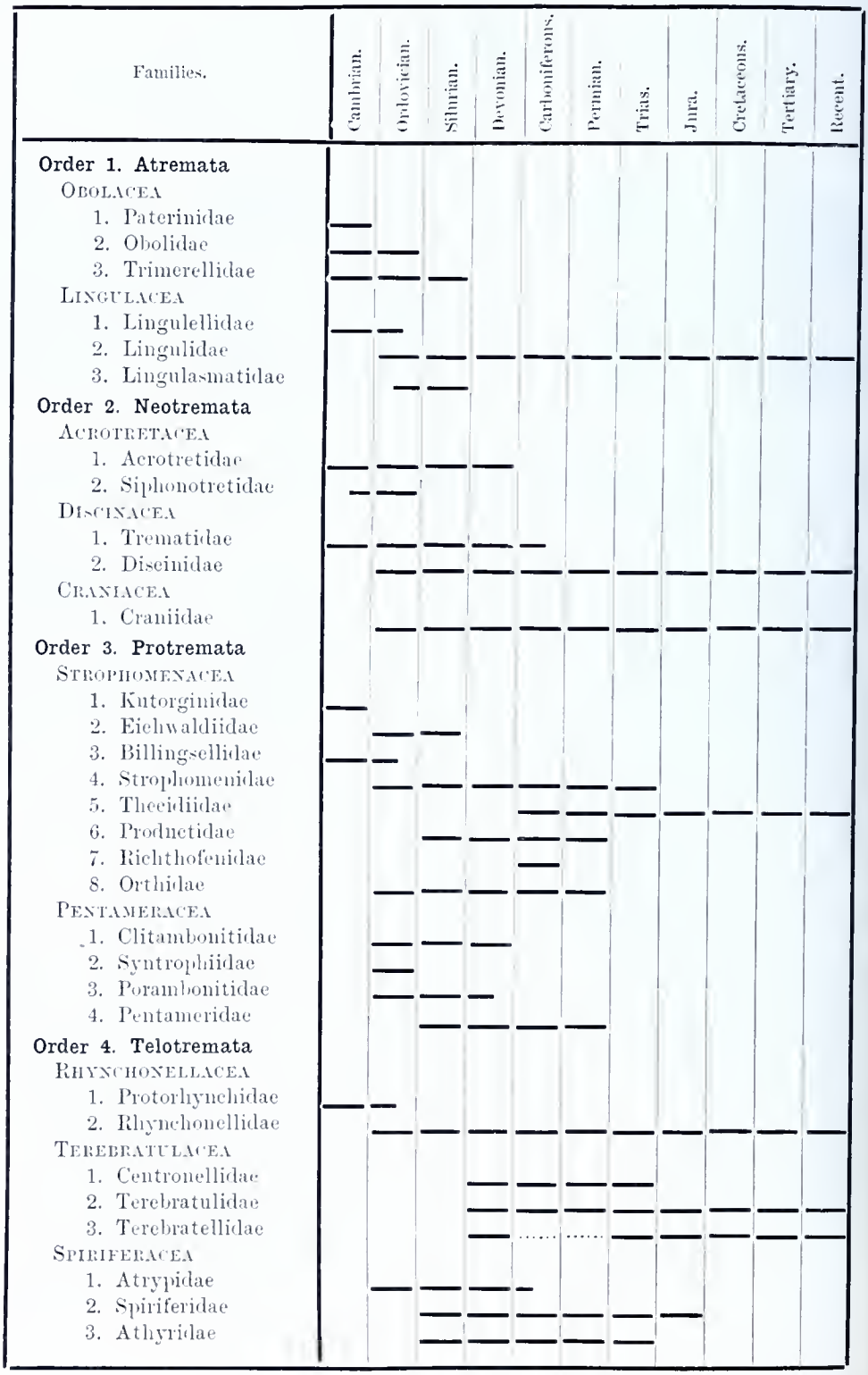
Camarospira, Hall and Clarke. Like *Meristella*, but with a small spondylium supported by a median septum, to which is attached only the pedicle muscle. Devonian; North America.

Range and Distribution of the Brachiopoda.

Owing to their great abundance, world-wide distribution, and remote antiquity, as well as their excellent state of preservation, Brachiopods occupy a very conspicuous rank among extinct Invertebrates, and furnish us besides with a large number of important index fossils. The calcareous composition of their shells enables them to resist the destructive action of the fossilisation process more successfully than the shells of Mollusks, which are composed for the most part of aragonite. Their value as index fossils, however, is somewhat detracted from owing to the difficulty of identifying numerous genera, without a knowledge of their internal structure.

The four orders into which the class is now divided are represented in the lowest Cambrian, or Olenellus zone, indicating that Brachiopods had their origin in Pre-Cambrian times. In the Lower and Middle Cambrian, the *Atremata* and *Neotremata* predominate; and although the *Protremata* are known in the Lower Cambrian by very typical species, it is not until the Upper Cambrian that the order becomes conspicuous. The *Telotremata* are

Table showing the Vertical Range of Brachiopods.



scarce throughout the Cambrian, but in the Ordovician, species and individuals abound.

In the Lower Cambrian (Olenellus beds), thirteen genera of Brachiopods are represented, occurring both in North America and in Europe. A marked increase is apparent toward the close of the Cambrian, and in the Ordovician and Silurian, where the climax of their diversity is reached, upwards of 2600 species are known. These are distributed chiefly in North America and in Europe (Great Britain, Scandinavia, Bohemia, Russia, and Portugal); but numerous forms are also found in South America, Australia, China, and Eastern Siberia.

In the Devonian Brachiopods are scarcely less plentiful than in the Silurian, although a considerable number of genera, especially those belonging to the *Atremata* and *Neotremata*, have now disappeared. The most noted European localities where Brachiopods abound are the Eifel, Rhineland, Westphalia, the Hartz, Belgium, Devonshire, Boulogne sur Mer, Cabrières in the Cevennes, the Asturias, and the Ural. Canada and the Middle Western States of North America also yield great quantities of Brachiopods.

The Carboniferous of North America and its equivalent horizons in Europe and Eastern Asia, together with the so-called Permo-Carboniferous of the Salt Range of India and Armenia, are very rich in Brachiopod remains, especially those belonging to the *Productidae*, *Strophomenidae*, *Spiriferidae*, and *Rhynchonellidae*.

In the European Permian, the number of species of Brachiopods is reduced to about thirty, but in the Salt Range of India greater numbers occur. In the Alpine Trias, the *Terebratulidae*, *Rhynchonellidae*, and *Koninckinidae* attain an enormous development.

The Jurassic and Cretaceous Brachiopods belong almost exclusively to the *Terebratulidae*, *Rhynchonellidae*, and the *Thecidiidae;* the first two families in particular being represented by an astonishing number of species. The *Spiriferacea* become extinct in the Lias.

With the beginning of the Cenozoic era, Brachiopods are no longer a conspicuous group of fossils. The species occurring in the Tertiary are almost without exception generically identical with those now living, and scarcely exceed them in number. On this account they are devoid of practical interest or importance to the geologist.

[The credit for having revised and practically rewritten the translation of the entire Brachiopod chapter belongs to Mr. Charles Schuchert, of the United States National Museum. The classification adopted has been taken from his *Synopsis of American Fossil Brachiopoda*, now in press.—Trans.]

Sub-Kingdom VI. MOLLUSCA.[1]

(*Malacozoa*, Blainville; *Saccata*, Hyatt.)

THE *Mollusca* form a well-characterised, and, on the whole, remarkably homogeneous group of Invertebrates, which have existed since the earliest recognised advent of life upon the globe. Their progressive modifications afford us a most important guide to the successive stages of the evolution of organic life as preserved in the various geological horizons.

The *Mollusca* are characterised as a group by passing through a Trochosphere and a Veliger larval stage; by possessing bilaterally symmetrical, unsegmented bodies; a larval shell gland, from which a harder exoskeleton or shell is secreted, though not always permanently retained; a mouth,

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intestinal canal, and anus; a closed, but partly lacunary circulation, assisted by a heart with one or more auricles, and containing a usually colourless body fluid or haemolymph; a nervous system with at least three pairs of ganglia connected by commissures; sexual reproduction by eggs and spermatozoa; audition and equilibration provided for by otocysts; respiration by ctenidial or secondary gills, or by the tegumentary surface, which may be invaginated to form a pulmonary sac; locomotion by a muscular organ called the foot, or by special parapodial structures; the organs normally paired, and protected by a sac-like integument called the mantle; and the visceral sac having a tendency toward torsion, so as to become usually asymmetrical. Sexually Mollusks are usually dioecious; or, if monoecious, incapable of self-fertilisation.

Owing to the homogeneity of the group, its division into classes has been attended with some differences of opinion, depending upon the point of view, the anatomist laying more stress upon certain groups of characters, and the morphologist upon others. From a general standpoint, the *Mollusca* are readily divisible into four classes, as follows:—Pelecypods, Scaphopods, Gastropods, and Cephalopods. The first of these is well marked off from the rest by the absence of a distinct head and of a radula, and the two groups have been contrasted as *Glossophora* (or *Cephalophora*) and *Aglossa* (or *Lipocephala*). Recent researches tend to show that the *Pelecypoda* form a degenerate group, more nearly related to the Protogastropod than is the latter to the Protocephalopod; and that in any general arrangement, the Cephalopods are rather to be contrasted with the three other groups combined.

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Class I. PELECYPODA. Goldfuss.[1]

(*Lamellibranchiata*, Blainville; *Conchifera*, Lamarck; *Bivalvia* (Bonanni), Linne; *Lipocephala*, Lankester.)

Aquatic, bilaterally symmetrical, acephalous mollusks, protected by a pair of shelly valves, which are secreted by the lateral portions of the mantle, connected by a ligament, and moved by the contraction of muscles attached to the inner faces of the valves; feeding by ciliary action and destitute of a radula or jaw; breathing by lateral gills; imperfectly sensible to light and rarely provided with peripheral visual organs; possessing olfactory organs (osphradia), auditory and equilibrating organs (otocysts), tactile papillae, and a nervous system composed of ganglia united by nerves, but without a pedovisceral commissure; provided with an extensile, tactile, or locomotor organ (foot); a circulatory system containing haemolymph, and operated by a single or paired cardial ventricle and two auricles; a more or less convoluted intestinal canal, with its oral and anal extremities at opposite ends of the body; a stomach; paired nephridia, connected with the pericardium, and discharging independently of the rectum; reproducing without copulation, by eggs and spermatozoa; monoecious or dioecious; development external to the ovary; the post-larval stage protected by a prodissoconch, and sometimes exhibiting a special nepionic stage.

External Characters. *The Shell.*—The embryonic Pelecypod is provided with a saddle-shaped, single shell gland, which secretes a pellicle of the same form, upon which, at two points corresponding to the valves, calcification sets in independently. These rudiments remain connected across the dorsum

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for a time, by the uncalcified portion of the original pellicle, which develops into the ligament of the adult. The paired embryonic shell, corresponding to the protoconch of Cephalopods, has been named by Jackson the *prodissoconch* (Figs. 588, 589). In general these valves are very uniform in character, as seen on the tips of the uneroded valves in the adult. They are usually rounded or slightly pointed at the umbonal end, and have in their earliest stages a straight, rather long hinge line. In *Solemya* the prodissoconch is elongate, rounded at the ends, with the ventral and dorsal margins nearly parallel, much as in the adult shell. In *Pinna* the prodissoconch is globular, as in most bivalves. In *Unio*, *Anodon*, and *Philobrya*, a second or nepionic stage is traceable, owing to a semi-parasitic habit of the young, which leave the mother and become encysted on the fins or gills of fishes; during this period the shell

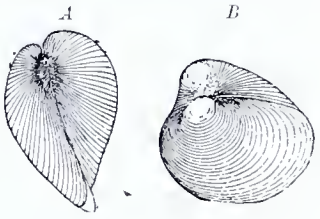


FIG. 588.

Ostrea Virginiana. Completed prodissoconch stage, viewed from the anterior end (*A*), and from the right upper side (*B*). $^{87}/_{1}$ (after Jackson).

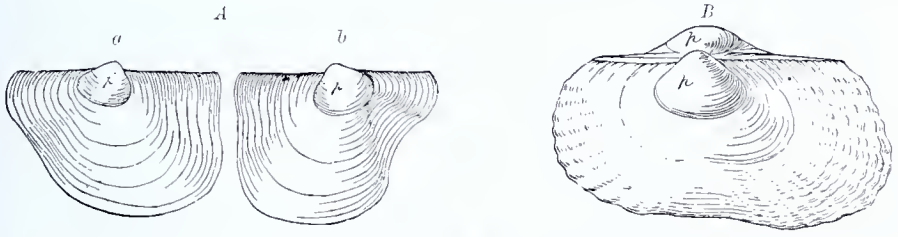


FIG. 589.

A, *Avicula sterna*. Young specimen, viewed from the left (*a*) and right (*b*) sides, the latter showing byssal sinus. $^{19}/_{1}$. *B*, *Arca pexata*. Very young, showing prodissoconch (*p*), succeeded by early dissoconch growth. $^{44}/_{1}$ (after Jackson).

remains stationary, though some development of the contained soft parts is in progress.

The bivalve shell reduced to its lowest terms comprises two convex pieces (the *valves*), attached to one another dorsally (1) by an elastic ligament external to the cavity of the two valves; and (2) by muscles and connective tissues which pass from the inner surface of one valve to the inner surface of the opposite valve. The contraction of the muscles brings the margins of the valves into close contact, thereby forming a hollow receptacle in which the soft parts of the animal are enclosed, and from which all obnoxious foreign matters may be excluded. The elasticity of the ligament, acting on the principle of the C spring, tends to separate the valves when the tension of the internal adductor muscles is relaxed. The substance of the valve is secreted by marginal glands around the edge of the investing tissue or mantle, and is subsequently reinforced by material supplied by secretion from the general surface of the mantle. As the animal grows and the original prodissoconch becomes too small to cover the soft parts, the valves are enlarged around the margins, so that each of them represents, fundamentally, a hollow cone. Since growth progresses more rapidly along some portions of the mantle than at others, the cones necessarily become oblique, arched, or cycloidally curved. The apex of the cone is formed by the beak or *umbo* of the shell, the base is the entire margin of the valve.

The shell of most Pelecypods is composed of several layers of distinct

structure. The external layer is usually thin, flexible, and dark-coloured, chiefly composed of a horny substance termed *conchiolin*. This layer is known as the *epidermis*, or more properly the *periostracum*; it is not easily corroded, and hence serves as a protection to the underlying calcareous layers. The outer calcareous layer is composed of prisms of calcite arranged more or less perpendicular to the external surface; the inner layer is made up of thin, more or less parallel lamellae of porcellanous or pearly texture, disposed at right angles to the general direction of the prismatic layer, and exhibiting the mineralogical characters of aragonite (Fig. 590). Besides the lamellar or prismatic structure, many forms show under the microscope minute, sometimes branched tubulation.

FIG. 590.

Vertical section of the shell of *Unio*. *c*, *b*, *a*, *a'*, the outer prismatic layer, showing successive increments of shell growth; *c*, *c'*, the inner lamellar strata. Highly magnified (after Carpenter).

The variations in shell substance are somewhat characteristic of different groups. The prisms vary greatly in size, the larger occurring in *Inoceramus* and *Pinna*, the smaller in the *Anatinidae* and *Myacidae*. The prismatic layer is wholly absent in the *Chamidae* and many other *Teleodesmacea*; in the *Pectinidae* and *Limidae* the prismatic layer is feebly developed and often recognisable only in young shells. In the *Rudistae* the prisms run nearly parallel with the outer surface. As aragonite is more soluble than calcite, it frequently happens in fossil shells that the layers composed of the former mineral have entirely disappeared, leaving only the calcitic layers. Pearls are merely loose portions of the inner layer secreted by the mantle surface, usually around foreign bodies which have reached the interior of the shell and set up irritation there.

In the majority of Pelecypods the valves form a nearly complete defence; in borers, burrowers, and a few degenerate types, the valves cover less and less surface in proportion to that which is bare; in a few the mantle is reflected so as to envelop more or less of the outer surface of the valves; and finally, in *Chlamydoconcha*, the valves are permanently internal, separately encysted, with the ligament isolated and encysted between them. No example is known of a Pelecypod absolutely destitute of valves in the adult state.

The valves of the shell are in general substantially equal; but sometimes they are unequal, especially in sessile or sedentary forms; and rarely they are spirally twisted, as in *Starelia* and *Spirodomus*. The *hinge* or *articulus* comprises the whole articulating apparatus,—hinge plate, teeth, ligament, etc.; the primitive hinge, which is coextensive with the ligament, is distinguished by Hyatt as the *cardo*. The *cardinal axis*, or right line forming the axis of revolution of the hinge, is parallel with the antero-posterior axis of the animal (as determined by a line drawn through the mouth and posterior adductor) in the ordinary *Teleodesmacea*; but in the winged *Prionodesmacea*, such as *Ostrea*, *Perna*, etc., the two axes are at a considerable angle with each other.

The dental armature is usually situated on the dorsal margin, which for

this reason is called the cardinal margin. It comprises the *teeth*, or projecting processes and sockets, usually alternating in the single valve, and opposite with respect to both valves. In the more modern and perfected types, the cardinal margin is reinforced by a vertical deposit of shell in the form of a lamina called the *hinge plate*, upon which the teeth are set. Above the hinge plate in each valve rise the beaks or umbones, which are usually curved toward the anterior end of the shell (prosogyrate), but are sometimes directed backward (opisthogyrate) or outward (spirogyrate).

According to the ordinary terminology, the *height* of a Pelecypod is measured on a vertical from the beaks to the ventral margin; the *length* corresponds to the greatest distance between the margins parallel with the antero-posterior axis above defined; and the *thickness*, or diameter, is measured by a line at right angles to the vertical plane descending from the cardinal axis (Fig. 592). When the shell is placed with the oral end anterior, the valves are termed right and left respectively, as viewed from above the articulus. The portion of the shell anterior to the beaks is usually shorter than that behind them, except in such forms as *Donax* or *Nucula*.

Viewed laterally, most Pelecypod valves may be divided into regions, corresponding in the main to the disposition of the internal organs. The *oral area* extends from the anterior end of the cardinal line to the anterior side of the pedal area. The latter is often marked by a swelling of the valves, and sometimes by a sinus (*Pholas*); it extends backward to a point where the branchial crest, radiating from the beaks, forms the anterior boundary of the *siphonal area*. The dorsal or posterior limit of the siphonal area is marked by an angle in the incremental lines; and above this, extending to the posterior end of the cardinal line, is the *intestinal area*. In the alate forms, like *Pteria*, the wings usually called anterior and posterior are really, with reference to the antero-posterior axis of the animal, dorsal and ventral.

In certain borers, the siphons are greatly produced outside the valves, and a calcareous tube is secreted, lining the burrow; the valves, situated at the anterior end of the boring, either lie free, or are partially or wholly fused with the tube. In the *Pholadidae* the naked portions of the animal between the edges of the valves are often protected by additional shelly pieces, which are organically separate from the valves; and some burrowers have the free ends of the siphons protected by leathery or calcareous shields. In the *Teredinidae* these shields are specially modified to protect the entrance of the burrow, and are called "pallets."

Ornamentation.—The external ornamentation of the valves is always a conspicuous character. It comprises (beside the concentric or incremental lines which indicate the successive additions to the shell margin, and are believed to coincide with resting stages during the process of growth) radial or concentric striae, ridges, ribs, folds, nodes, spines, or foliaceous processes. These are supposed to arise from temporary or permanent modifications of the mantle margins, such as papillae, minute tentacular, or proliferate processes. Other modes of ornamentation, such as that observed on the beaks of *Unionidae*, proceed from the serrate margin of the glochidial shell.

Above the hinge line, in archaic types, is an area often set off by an impressed line and called the *cardinal area*. In the more perfected modern forms this area is commonly divided; a heart-shaped space in front of the beaks, and bounded by a ridge or groove, being known as the *lunule*; and a

more elongated space extending backward from the beaks being designated the *escutcheon*. Both areas often have a special sculpture, differing from that of the remainder of the shell.

Another form of ornamentation is sometimes found on the opposed inner margins of the valves, away from the hinge line, as in *Woodia* (Fig. 707), or *Transenella;* it probably aids in preventing a lateral displacement of the valves. In general, all ornamentation may be confidently ascribed to a dynamic origin.

Internal Characters. *Soft Parts.* — The Pelecypod body is enclosed within two thin, partly fleshy mantle lobes, which are united or continuous below the cardinal margin, and open or partially united at other points on their periphery. Within the mantle lobes are the visceral mass including the internal organs, the gills or *ctenidia*, the foot, and the palpi. When the mantle edges are united so as to form tubes for the entrance and discharge of water, such tubes are called *siphons*. These organs, all of which have been utilised in classification, will be considered separately.

The *mantle* is closely applied to the surface of the valves, and is usually attached to them along a line near its periphery. This line is indicated by a continuous scar or impression upon the inner surface of the valves, termed the *pallial line*. Outside the pallial line a portion of the margin is free and usually thickened. In it are contained the glands which secrete the shell, and also pigment glands; it is ornamented by papillae, tentacular processes, etc., and is sometimes furnished with visual organs of a primitive sort. Certain archaic forms had no distinct pallial line, the mantle being organically attached over a more or less irregular area. The ends of the pallial line are commonly continuous with the scars of the adductor muscles.

The majority of Pelecypods have two *adductor muscles*, and are distinguished accordingly as Dimyarian, or Homomyarian; in some the anterior muscle is absent or degenerate (*Monomyaria*); and in others an intermediate condition obtains (*Heteromyaria* or *Anisomyaria*). The number and position of the adductors was formerly accepted as a fundamental feature in classification, although many difficulties were presented by exceptional cases. Recent researches have shown that an absolute foundation for classification cannot be afforded by the number of adductors; but still, if allowance be made for degeneration caused by inequilaterality, torsion, and other causes, the general myarian-types harmonise fairly well with the larger divisions based on the totality of characters.

The *visceral mass*, as a rule, occupies the upper portion of the shell, and contains the heart, intestinal canal, generative organs, renal and other glands. The rectum usually lies above the posterior adductor, and discharges into the anal siphon, when present. The mouth is placed at the forward end of the visceral mass below the anterior adductor, and is commonly furnished on each side with a pair of leaf-like expansions of the integument called *palpi*, which are ciliate internally, and serve to conduct alimentary matter from the gills to the mouth. Palpi are seldom wanting, and their form and character remains fairly constant throughout a number of groups. The mouth itself is unarmed, and the alimentary canal is more or less bent, usually exhibiting a dilation which is regarded as the stomach.

The Foot.—From the ventral surface of the visceral mass projects an extensile muscular organ, known as the *foot*, which is capable of being pro-

truded beyond the margins of the valves, or entirely retracted within the mantle lobes. The muscles serving to move this organ are inserted upon the shell near the adductor scars, leaving small accessory impressions. In a large majority of bivalves, the foot has the familiar hatchet-shape from which the class name is derived, but as an organ of locomotion, tactile use, and possibly prehension, it is modified for special uses in many forms. A few mollusks, such as *Ostrea*, have the foot altogether aborted, though remnants of its retractor muscles exist and are attached to the valves; and in some cases (*Pholadomya*, *Halicardia*) an accessory foot-like organ, or "opisthopodium," is developed at the posterior end of the visceral mass.

In many Pelecypods the foot is provided with a gland secreting horny matter which solidifies in threads after extrusion, forming a fixative tuft or cable called the *byssus*, by which the animal adheres to extraneous objects. Some sessile genera have the byssus more or less calcified, when it forms a shelly plug closing a sinus or foramen in one of the valves through which it passes. Many of the *Pectinidae* have a comb-like series of denticles (*ctenolium*) on the edge of the byssal sinus, in which the byssal threads rest. In permanently sessile forms, the byssus is usually absent.

Gills.—On either side of the visceral mass above the foot and usually extending from the palpi to the posterior adductors are the gills or *ctenidia*. In a general way the ctenidium is composed of a stem carrying a nerve and blood-vessel, from which on each side leaflets or slender filaments are given out laterally. In the more archaic types (*Nucula*, *Yoldia*, *Solemya*) these gills are plate-like, not organically united except by the stem, though in some cases attaining a solidarity as a mass, by the interlocking of very large cilia, distributed in bands or patches on the opposed surfaces of individual plates.

These plate-like gills are termed foliobranchiate or protobranchiate. According to their structure, other types of gills are intermediate between these and the so-called "filibranchiate," in which the plates are elongated and strap-like, and the "reticulate," in which the filaments are united by cross conduits in a net-like manner. Attempts have been made to employ the various types of gills as fundamental characters in classification, but experience has shown that they cannot be depended upon as the exclusive basis of any systematic arrangement.

Siphons.—When the mantle lobes are united, two posterior openings, more or less tubular, are always present (Fig. 591). The dorsal tube, called the *dorsal* or *anal siphon*, serves for the discharge of water which has been inhaled through the ventral or branchial siphon, carried to the gills, deprived of its oxygen and edible particles, and then expelled. The anal siphon also carries effete matters from the rectum, and sometimes ova are discharged in the same way. The tubes are sometimes adherent or enclosed in the same envelope, and sometimes separate to their base; in general, however, a septum or partition exists between the two passages, thus avoiding the mixture of the two currents. The siphonal septum is frequently carried forward internally, or supplemented by a junction of the gills in such manner as to form a

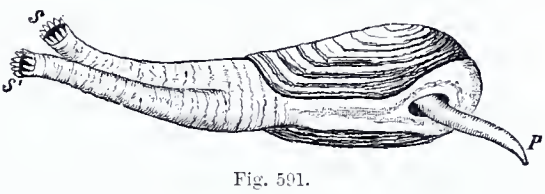


Fig. 591.

Saxicava arctica, Lam. Animal with closed mantle edges, showing foot (*p*), protruding from the pedal opening, and anal (*s*) and branchial (*s'*) siphons. Natural size.

practically continuous partition between the anal and branchial regions within the mantle. The siphons are always contractile, and, except in sedentary burrowers, usually retractile within the shell.

The siphons, being a local modification of the mantle margin, receive their musculation from the same source. In general, the muscles have spread inward, *pari passu* with the increase in length of the organ to be retracted, and their insertion on the valve leaves an angular scar called the *pallial sinus*, which is an important aid in classification of the minor groups. It has sometimes been assumed that the absence of this sinus was evidence of the asiphonate character of the species, but the example of *Lucina*, *Cuspidaria*, and several other siphonate forms which have no pallial sinus show that this is not necessarily true. Formerly, when the character of the pallial line was regarded as of prime importance, the Pelecypods with a sinus were called *Sinupalliata* (Fig. 592), and those without, *Integripalliata* (Fig. 593).

The Hinge.—The origin both of the hinge structure and the ornamentation of the shell can be perhaps best understood by a consideration of what is

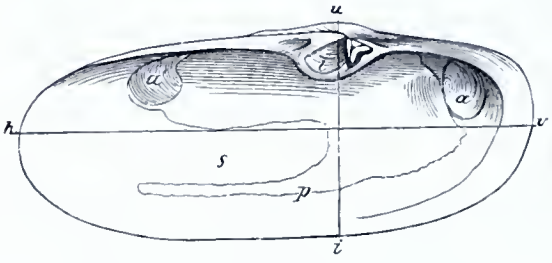


Fig. 592.

Lutraria elliptica, Roissy. Interior of left valve showing pallial line (*p*); pallial sinus (*s*); anterior (*a*) and posterior (*a'*) adductor scars; and resiliifer (*l*). *hc*, Length; *vl*, Height of the shell. ⅔ natural size.

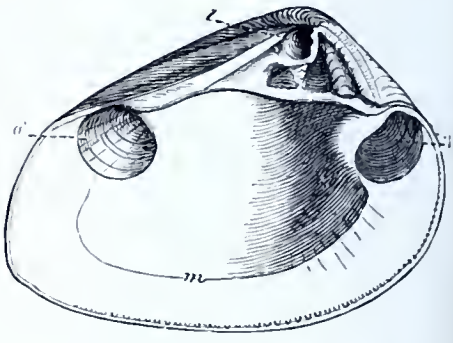


Fig. 593.

Crassatellites plumbea, Chem. sp. Interior of left valve showing entire pallial line (*m*); anterior (*a*) and posterior (*a'*) adductor scars; and resiliifer (*l*). ⅔ natural size.

known regarding the archetype of the class, and by noticing the changes that have since been introduced. The original protopelecypod was small, thin, symmetrical, sub-circular or oval, with a short external ligament equally disposed on each side of the beak along the hinge line. The mantle was not uniformly attached to the shell along a pallial line, as in modern Pelecypods, but adhered more or less irregularly and was not provided with extrusile siphonal tubes. The adductor muscles were sub-equal, symmetrical, and situated high up in the valves. The surface of the valves was smooth, or (probably in connection with the development of tactile papillae on the mantle edge) radiately ribbed. These conclusions are justified not only by inference and by recent investigations on the morphology of the prodissoconch, but by the characters of the most archaic Pelecypods, summarised by Neumayr under the name of *Palaeoconcha*.

Since the general form of the Pelecypod depends upon its principal anatomical characters (the size, number, and position of the muscles, the presence, size, and character of siphons, byssus, etc.), then, to a certain limited extent, especially in the modification of the primitive simple Palaeoconchs, it is plain that the differences of form would march with the respective anatomical differences. For example, those forms which retained the simple

open mantle and sub-equal adductors would continue to be of a rounded and symmetrical shape; while those which tended to produce elongate siphons, or in which marked inequality of the adductors was developed, would probably present more elongate or triangular outlines. The differences of form would necessarily react upon the developing hinge, from the inevitable operation of physical laws, and thus tend to produce in connection with particular lines of evolution of form, particular types of hinge.

The recent researches of Bernard and Simroth have developed the fact that in some Pelecypoda the ctenidium originates as a lateral plate, which becomes transversely folded, and in which the reticulate form results from subsequent perforations between the folds, and not from the concrescence of originally separate filaments, as has been hitherto supposed to be the invariable mode.

Neumayr has shown that, among the *Palaeoconcha*, ribbing existed in various species along the dorsal as well as the other margin, and that it produced denticulations there; and that when these denticulations had become a fixed specific character, the ribbing disappeared from the area above the hinge margin.

In this way (as analogically in the recent *Crenella et al.*) the initiation of the processes called *hinge teeth* began. Such projections, interlocking at a time when the serrations of the other margin of the open valves could be of little assistance in securing rigidity, offered a means of defence of the greatest importance when fully developed by natural selection, one which would be useful at every stage of development, but would increase in usefulness with increase in size. In fact, this was just such a feature as would lend itself to the fullest operation of natural selection. Once well initiated, its progress was inevitable, and its variety and complexity only a question of time.

Very recent studies by Bernard of the development of hinge teeth in nepionic Pelecypods of many groups, show that in most if not all Prionodesmacea and some Teleodesmacea there is first developed on each side of the ligament (or behind it in *Ostrea*) a series of transverse denticulations or minute taxodont teeth, forming what has been called a *provinculum* or primitive hinge, independent (so far as yet observed) of the permanent dentition. The latter begins subsequently by the development of distinct laminae on the hinge plate. In the Teleodesmacea, toward the ends of the hinge plate the primitive lamellae originate below the provinculum or in its absence, and grow proximally. The inner ends of the anterior lamellae become hooked, and these hooks separate from the distal portions which remain to form the anterior laterals, while the hooks develop into the cardinals, and the posterior lamellae into the posterior lateral teeth. The facts point, of course, to the provinculum as representative of the primitive hinge as observed in many Palaeoconchs; but the gap between the provinculum and the beginnings of the permanent dentition, indicates a suppression of certain developmental stages which only further researches can supply.

The dynamical origin of the shelly processes of the hinge, which we call *teeth*, has only recently attracted attention. In this work Neumayr led the way, and his contributions have been most valuable; yet, as often happens with pioneer work, he failed to grasp fully all the details of the subject, and the nomenclature he proposed has required revision. Several groups or kinds of teeth can easily be distinguished. These are not necessarily funda-

mental, since the teeth, being largely moulded by the dynamics of their situation, change with the influences to which their form is due, and in course of time may become obsolete from disuse (*Anodon*), or modified so as to simulate the teeth of groups with widely different pedigree (*Nucula*, *Mutela*; *Plicatula*, *Trigonia*). In general, however, at any given time, the types of teeth are good evidence of the relationship of forms to which they are common, especially if the development from the younger stages of the species under comparison proceeds along similar lines.

The modifications of the hinge now generally recognised are as follows:—

In the *Taxodonta* the hinge is composed of alternating teeth and sockets, mostly similar, and frequently forming a long series, as in *Arca* (Fig. 594, *A*) or *Leda* (Fig. 594, *B*). The *Schizodonta* have heavy, amorphous, variable teeth, often obscurely divided into sub-umbonal (pseudocardinal) and lateral (posterior) elements, as in *Trigonia* (Fig. 595), *Unio* (Fig. 596), and *Schizodus*.

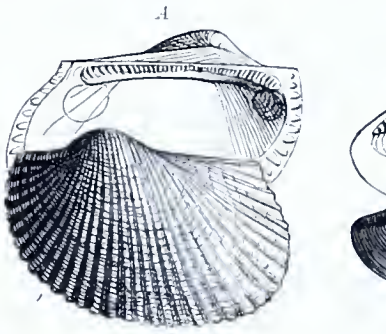


Fig. 594.

Taxodont hinges. *A*, *Arca*, with external ligament. *B*, *Leda*, with internal resilium.

Fig. 595.

Schizodont hinge. *Trigonia pectinata*, Lam. Recent; Australia.

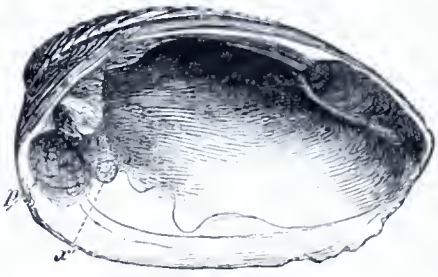


Fig. 596.

Schizodont hinge of *Unio Stachei*, Neumayr, showing pseudocardinal and lateral teeth. Pliocene, Slavonia.

In the *Isodonta* the original Taxodont provinculum is often replaced in the adult by a hinge structure derived from two ridges (the "auricular crura") originally diverging below the beaks. This becomes, in the most specialised forms, an elaborate interlocking arrangement of two concentric pairs of teeth and sockets, which cannot be separated without fracture, as in *Spondylus* (Fig. 669). In less specialised forms, such as *Pecten*, the provinculum becomes obsolete, and the crura only partially develop.

The *Dysodonta* of Neumayr was originally a heterogeneous group, and the term is now restricted to that division having a feeble hinge structure, whose origin is more or less palpably derived from external sculpture impinging upon the hinge line, as in *Myoconcha* (Fig. 597), *Pachymytilus* (Fig. 598), and *Crenella*.

The preceding groups, together with the edentulous *Solemyacea*, constitute the order *Prionodesmacea*, which is knit together by community of descent still traceable in their anatomy.

The *Pantodonta* are a small group of Palaeozoic forms whose dentition

partakes of the synthetic character of the more archaic forms, while foreshadowing the future Teleodont types. In this group the laterals may exceed a pair in a single group, which is never the case in the modern types. *Orthodontiscus* and *Allodesma* are examples.

The *Diogenodonta* are the modern and perfected forms in which there are differentiated lateral and true cardinal teeth upon a hinge plate, the former never exceeding two nor the latter three in any one group. *Astarte* (Fig. 705), *Crassatellites* (Fig. 593), and *Corbicula* (Fig. 712) are examples.

Fig. 597.

Dysodont hinge of *Myoconcha striatula*, Goldf. Lower Oolite; Bayeux, Calvados. 1/1.

Fig. 598.

Dysodont hinge of *Pachymytilus petasus*, d'Orb. Coral Rag; Coulange-sur-Yonne, France. 2/3.

The *Cyclodonta* exhibit extreme torsion in their dentition, which curves out from under the beaks and is not set upon a flat hinge plate. *Isocardia* (Fig. 757), *Tridacna*, and *Cardium* (Fig. 752) are examples.

In the *Teleodonta* are found the most highly perfected types of hinge. The characters of the less specialised forms hardly differ from those of the *Diogenodonta*, but they are placed here on account of their obvious affinities as shown by other characters. The most specialised forms add to the ordinary cardinal series of the *Teleodesmacea* (10101) either a roughened area, as in *Venus;* a series of extra cardinals, as in *Tivela;* or accessory lamellae, as in *Mactra*, making the hinge more complicated or efficient. *Cytherea* (Fig. 760), *Mactra* (Fig. 775), *Venus* (*mercenaria*), and *Tivela* are examples.

Several of these forms were included by Neumayr in a group called *Desmodonta*, which he founded on such types as *Mactra* under a misapprehension as to the character of the hinge; almost all of the others were included in his *Heterodonta*, which, construed strictly, would take in all dentiferous Pelecypods, since the alternation forming its essential character is inseparable from the possession of functional teeth.

The *Asthenodonta* comprise borers and burrowers in which the teeth have become obsolete from disuse. *Corbula* (Fig. 779), *Mya* (Fig. 778), and *Pholas* (Fig. 784) are illustrative types. In the last-named a remarkable development of the sub-umbonal attachment of the mantle has produced a myophore which is sometimes wrongly interpreted as a tooth. The exceptional development of this feature is explained by the dynamics of Pholad existence.

The above groups form the order *Teleodesmacea*, and dentally are intimately related. Recent studies by Bernard[1] as to the genesis of individual teeth among members of this order show great uniformity in the early stages. But inasmuch as these observations are dependent upon the mode of growth

[1] *Bernard, F.*, Sur le developpement et la morphologie de la coquille chez les lamellibranches (Bull. Soc. Geol. France [3], XXIII.), 1895, and XXIV., 1896.

in highly specialised Pelecypods, in which the development of teeth is largely secondary, care must be taken not to confound these processes with those by which hinge teeth were originally initiated in edentulous Protopelecypods.

Finally, in the *Anomalodesmacea* we have a tribe of burrowers which have preserved to the present day some of the features which characterised the edentulous Protopelecypods of ancient geological time. The small teeth of the nearly edentulous hinge may sometimes be associated with the submersion of the resilium and the development of a chondrophore, but in other cases they may be the remnants of hinge teeth acquired in the ordinary way early in the geological history of the group.

Dental Formulae.—For the purpose of recording compactly the number and character of the teeth in adult Pelecypods, a formula has been suggested by Dr. Steinmann, which, somewhat amplified, is as follows :—

Let L represent the left and R the right valve, and the teeth be represented by units ; the sockets into which teeth of the opposite valve fit by zeros ; the resilium or chondrophore by C ; the laterals by l ; the elasping laminae which receive the laterals by m, if single ; if double, by m2. Where two Taxodont rows meet on one hinge margin and are not separated by a resilium, as in *Pectunculus*, let their junction be marked by a period. Obsolete or feeble teeth may be represented by the italicised symbol for normal teeth. For amorphous, interlocking masses, which cannot be classified as teeth, and are of varied origin, the symbol x is adopted. The enumeration begins at the posterior end, and the right-hand end of the formula is always anterior.

Thus, types of Teleodont dentition may be represented as follows :— *Astarte borealis*, $\frac{\text{L}m0101l}{\text{R}l\,1010lm}$; *Crassatellites antillarum*, $\frac{\text{Lmc101}\,l}{\text{R}\,l\,\text{c}010m}$; *Venus mercenaria*, $\frac{\text{Lx01010}}{\text{Rx10101}}$ (in this case x represents the rough area below the ligament).

In investigating the genesis of the individual hinge teeth in various genera of the *Teleodesmacea*, Messrs. Munier-Chalmas and Bernard have adopted the following formula, which expresses at once the origin and position on the hinge of the several teeth. In the majority of cases the teeth appear to be derived from two primitive pairs of lamellae in each valve, one pair anterior and one posterior. Each adult tooth is designated by an arabic numeral corresponding to the primitive lamella from which it is derived, with *a* for the anterior and *b* for the posterior tooth when a single primitive lamella gives rise to two teeth. The laterals are counted from below upward in Roman numerals, the odd numbers belonging in every case to the right, and the even numbers to the left valve. If it is necessary to name a socket it receives the designation of the tooth which occupies it, supplemented by an accent (′). A and P stand for anterior and posterior, L for lateral, and CA for cardinal teeth. Finally, if a tooth disappears, its place is indicated by a zero with an index showing which particular tooth it was. The numeration of the cardinals always begins with the right median cardinal tooth. Thus, CA1 = median cardinal of the right valve, CA2*b* = left median cardinal derived from the posterior part of primitive lamella number two ; LA I = ventral anterior lateral, LP III = dorsal posterior lateral, etc.

Ligament.—The ligament which unites the two valves, as stated above, is primitively continuous with them as the uncalcified part of the primitive pellicle secreted by the original shell gland ; it is therefore neither external nor internal. With its subsequent differentiation, and the thickening of the

valves by calcification deposited about it, it occupies a depression in the cardinal margin which Bernard has regarded as internal. In a sense it is internal, but its position at this stage is not significant, and there is no fundamental difference between the cases. The differentiation in function and structure which we find in the adult between the ligament, properly so-called, and the "internal ligament" or *resilium*, is a later development.

The ligament may be regarded as a fundamental character of Pelecypods, and is universally present, though in some cases as a mere degraded rudiment (*Pholadacea*); it may be separated from the valves and functionless (*Chlamydoconcha*), or present only in the young stages and lost through specialisation due to the sessile habit (*Rudistae*).

As the most important factor in the mechanism of the valves, the ligament has undoubtedly developed with the evolution of the class, and its chief modifications date from the earliest period in the life-history of the group. The function of the original ligament was that of an external link between the valves having the essential nature of a C-spring. That is, the insertion of the ligament edges on the cardinal margins, or, at a later period, on thickened ridges or *nymphae* by which these margins are reinforced to bear strains, resulted in the following conditions:—The valves being held together and, in closing, approximated by the contraction of the adductor muscles, the preservation of their precise apposition, marginally, is due to a rotary motion, exerted along the axis of the ligament, which pulls the attached edges of the ligament nearer to each other and exerts a strain on its cylindrical exterior. This operation, with a thin ligament, involves a tensile strain on the whole cylinder; with a thick ligament the external layers are strained and the internal layers compressed, so that, to the tensile elasticity of the external layers is added the compressional elasticity of the internal portion. The result of the differing strains to which the several layers of the ligament are subjected brings about a difference of structure, and, whenever the ligament becomes deep-seated, there is a tendency for the respective parts to separate along the line where the two sets of strains approximate. We then have two elastic bodies, operating reciprocally in opposite directions, the outer or ligament proper tending to pull the valves open to a certain distance corresponding to its range of tensional elasticity; and the other or *resilium* (for which the objectionable terms "cartilage" and "internal ligament" have been used) tending to push them open to an extent corresponding to its range of expansion.

The ligament proper is of a more or less horny nature, tough, and semi-translucent beneath its external surface. When dry it has a vitreous fracture, and often shows hardly any fibrous texture.

The resilium is distinctly lamellar or composed of horny fibres, which are apt to give a pearly sheen to its broken surface. There is often a more or less extensive intermixture of lime in its substance, which may be diffused, or may be especially concentrated along the median plane. As may be seen by examining the unbroken resilium (as in *Mactra*), this organ in such cases has something of an hour-glass shape; the ends which fit into the "cartilage pits" or *resilifers* being more expanded than the centre between them. The deposit of lime in the form of an accessory shelly piece, usually termed the *ossiculum* or *lithodesma*, serves for the reinforcement of the resilium.

For the type of ligament which extends on both sides of the beaks,

Neumayr adopts the designation *amphidetic;* and for the more perfected type which has been withdrawn wholly behind the beaks, he employs the term *opisthodetic* (Fig. 599). *Glycimeris* offers a conspicuous type of the amphidetic ligament; *Tellina* and *Venus* exemplify the opisthodetic arrangement. In many bivalves a lozenge-shaped cardinal area extends amphidetically between the beaks, while the ligament is wholly posterior, being visible as an oblique triangular space, with its apex at the umbonal point and its base at the hinge line, as in *Avicula*. Nearly every stage in the recession of the ligament can be observed, from truly central to posterior, in *Lima* and its allies.

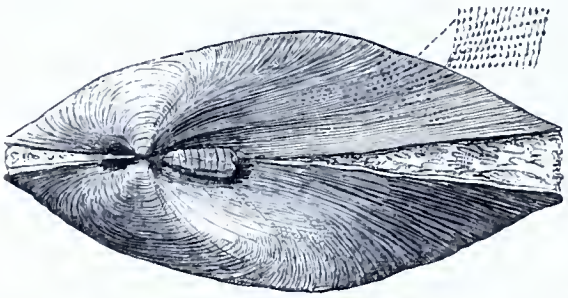


Fig. 599.

Homomya calciformis, Ag. With well-preserved external, opisthodetic ligament. Lower Oolite; near Bayeux. 2/3.

The most perfected type of ligament is that which may be compared to a cylinder split on one side, and attached by the severed edges, one edge to each valve. This type is known as *parivincular* (*Tellina*, *Cardium*); its long axis corresponds with the axis of motion or vertical plane between the valves, and in position it is usually opisthodetic. Another form is like a more or less flattened cord extending from one umbo to the other (*Spondylus*, *Lima*), with its long axis transverse to the plane of the valve margins and the axis of motion. This is called *alivincular;* it may be central or posterior to the beaks, but, unless very short, is usually associated with an amphidetic area. Lastly, a third form must be noted which consists of a reduplication of the alivincular type at intervals upon the area (*Perna*, *Arca*, *Fossula*), either amphidetically or upon the posterior limb of the cardinal margin. This is designated as *multivincular*, and is developed out of the alivincular type.

In some forms with a rigid hinge and internal resilium, the ligament may degenerate into its archaic epidermic character, as in some species of *Spondylus*. It is impossible to draw a sharp line between these and similar forms in which the ligament is not quite reduced to the state of epidermis, as in some species of *Ostrea*. The cardinal area above referred to is in part the morphological equivalent of the lunule of Teleodont Pelecypods. In general, when the ligament has become opisthodetic, the remnant of the area in front of the beaks forms the lunule and may be called prosodetic. The amphidetic area is an archaic feature which has been lost by the more specialised types of modern bivalves, and its gradual disappearance may be traced in various Prionodont genera.

The separation of the ligament and resilium has been described as due to mechanical causes.[1] In cases where the resilium becomes submerged from between the valves, the area of attachment of its ends in thin-shelled forms is more or less thickened and assumes a spoon-like form projecting from the hinge plate, termed the *chondrophore* or *resiliifer;* this is often reinforced by a special prop or buttress called the *clavicle*. It has been suggested by Neumayr that part of the armature of the hinge, in the shape of teeth, is due to deposits

[1] Amer. Journ. Science [3], vol. XXXVIII., 1889, pp. 448-451.

made parallel to or induced by the presence of the chondrophore and resilium.

There is some reason to think that the presence of the resilium in *Pecten* and *Spondylus* may be connected with those changes of the auricular crura which lead to the assumption of dental functions by the latter. But it is well known that submergence of the resilium occurs independently in many unrelated groups of bivalves; and it is probable most of them were previously dentiferous and still retain their teeth, although more or less modified or displaced, while the edentulous genera seldom show any teeth which appear to owe their existence solely to the presence of a chondrophore. The nearest approach to a hinge composed of dental laminae of such an origin is found in *Placuna*, *Placenta*, and *Placunanomia*, together with the *Spondylidae* already mentioned.

Classification.—The class *Pelecypoda*, which comprises about 5000 recent and twice as many fossil species, appears to be divisible into three ordinal groups: *Prionodesmacea*, *Anomalodesmacea*, and *Teleodesmacea;* of which the third represents the most perfected and developed (though not always the most specialised) modern type of bivalve. There seems little reason to doubt that all these orders are descended from a Prionodesmatic radical or prototype, and that for various reasons the first and second retain more evident traces of this origin than the third.

For convenience of comparison the characteristics of these orders will be stated here.

Prionodesmacea.—Pelecypods having the lobes of the mantle generally separated, or, when caught together, with imperfectly developed siphons; the soft parts in general diversely specialised for particular environments; the shell structure nacreous and prismatic, rarely porcellanous; the dorsal area amphidetic or obscure, rarely divided into lunule and escutcheon, and when so divided, having an amphidetic ligament; ligament variable, rarely opisthodetic; nepionic stage usually with a taxodont provinculum; permanent armature of the hinge characterised by a repetition of similar teeth upon the hinge line, or by amorphous schizodont dentition; habits active, sessile or nestling, not burrowing; monoecious or dioecious.

This group, originating with the earliest forms, has retained many archaic features through immense periods of geological time, although occasionally developing remarkable and persistent specialisations. Notwithstanding most of its subdivisions have arrived at a notable degree of distinctiveness, intermediate forms of ancient date connect them all, more or less effectively, with the parent stem.

Anomalodesmacea.—Pelecypods having the mantle lobes more or less completely united, leaving two siphonal, a pedal, and sometimes a fourth opening between them; siphons well developed, always at the posterior end of the body; two subequal adductor muscles; the shell structure nacreous and cellulo-crystalline, rarely with a prismatic layer; the area amphidetic or obscure, rarely distinctly divided; the ligament usually opisthodetic, generally associated with a separate resilium, chondrophores, and lithodesma; valves generally unequal, the dorsal margin without a distinct hinge plate, armature of the hinge feeble, often obsolete or absent; rarely with lateral laminae or well-developed dental processes; usually burrowing, hermaphrodite, and marine.

This group is intimately related to many of the *Palaeoconcha*, except as regards the presence of a pallial sinus. It retains many archaic features, and includes several of the most specialised modern forms. Through the *Anatinacea* it approximates the Myacean *Teleodesmacea*. It is peculiar in the possession of a lithodesma, and in the structure of its gills and hinge. The forms with a reticulate gill have it of a different type from the reticulate gills of the other orders; those which retain a modified foliobranch gill have it different from the foliobranch gill of Prionodesmacean groups.

There are no forms with a filibranchiate gill, or with a typically fully developed reticulate gill.

Teleodesmacea.—Pelecypods with reticulate gills, the ventricle of the heart embracing the rectum; having the mantle lobes more or less connected and usually possessing developed siphons; the adductors practically equal; the shell structure cellulo-crystalline (porcellanous) or obscurely prismatic, never nacreous; the dorsal area, when present, always prosodetic or divided into lunule and escutcheon; ligament opisthodetic, with or without separate resilium; without a lithodesma, rarely with external accessory shelly pieces; nepionic stage usually without a Taxodont provinculum; permanent armature of the hinge characterised by the separation of the hinge teeth into distinct cardinals and laterals; the posterior laterals, when present, placed behind the ligament; the animals active or nestling, sometimes sessile, but rarely sedentary burrowers, rarely inequivalve, usually possessing a hinge plate and a pallial sinus; sexes usually separate.

It is doubtful if this group is represented in the Palaeozoic rocks, especially below the Carboniferous, though genera belonging to it are foreshadowed by some of the Palaeoconchs. Although most of the Teleodonts live embedded in the surface of the sea-bottom, they retain their ability to migrate, and only a few extremely specialised forms inhabit permanent burrows of their own construction. They are sometimes commensal in the burrows of other animals. Similarly, few of them fix themselves permanently by a byssus, although often byssiferous, especially when young. With the exception of a few specialised forms they possess a pair of direct and reflected branchial laminae on each side of the body, frequently united behind the foot, forming an anal chamber; the two sets on one side usually of unequal size, and of the reticulate type. None are known with typically foliobranch or filibranch gills, although some abyssal forms have archaic sub-foliobranchiate ctenidia.

There remains a small group of fossils, difficult to refer to a place in the system, yet characterised by several features in common; these have been named by Neumayr *Palaeoconcha*, and are defined by him as follows:—

Palaeoconcha.—Prototypic Pelecypods, with thin shells, a simple or obscure pallial line, sub-equal adductor scars placed high in the valves; dorsal area absent or amphidetic; ligament external, variable; hinge margin edentulous or with polymorphous teeth formed by modifications of the margin and not set upon a hinge plate.

While the forms included here are not always actually the most ancient, yet in their modifications they indicate clearly the origin of many subsequently developed structures found in Pelecypods of a more modern type; and owing to their undifferentiated polymorphic character are difficult to assign a place in any classification based on more highly developed forms. There is little doubt that some of these show Taxodont affinities, and others recall *Pholadomya*: but the final discussion of these puzzling forms awaits greater knowledge of them and other early bivalves. It is to be understood that the places assigned them in the present systematic arrangement must be more or less provisional. Neumayr included in this group the following families:—

Vlastidae.	*Praecardiidae.*	*Solenopsidae.*
Cardiolidae.	*Silurinidae.*	*Grammysiidae.*
Antipleuridae.	*Protomyidae* (including possibly	*Posidonomyidae.*
Lunulicardiidae.	the recent *Solemya*).	*Daonellidae.*

The pelagic *Planktomya Henseni*, recently described by Simroth, presents many of the characteristics of the Palaeoconchs. The posterior cardinal margin is denticulate, the ligament internal, and the gills are represented by a single lateral plate parallel with the longer axis of the shell on each side; a type elsewhere only known in connection with the younger stages of *Scioberetia*.

Order 1. PRIONODESMACEA. Dall.

I. (Palaeoconcha, p.p. Neumayr).[1]

Family 1. Solemyacidae.

Shell Soleniform, equivalve, low-beaked, edentulous, gaping, with the anterior end longer and the epidermis conspicuous, exceeding the valves; area obscure or none; ligament amphidetic, parivincular, becoming internal posteriorly; mantle lobes united ventrally, attached in front to the epidermis and valves by a broad surface, leaving no distinct pallial line; a single posterior siphonal and anterior pedal foramen in the mantle; adductors sub-equal, with a thickened ray in front of the posterior scar; animal dioecious, marine, burrowing. Silurian to Recent.

Solemya, Lam. Carboniferous to Recent, rare in all horizons. *? Orthodesma*, Hall. Silurian. *Janeia*, King, shorter and less inequivalve, may include most of the Palaeozoic species hitherto referred to *Solemya*. *Clinopistha*, Meek and Worthen, from the Carboniferous, is also allied, and *Dystactella*, Hall, is united with it by Zittel. *Phthonia*, Hall, from the Devonian, is placed here by Ulrich.

Family 2. Solenopsidae. Neumayr.

Shell thin, elongate, equivalve, with very anterior beaks; the hinge edentulous, ligament parivincular, external; pallial line not sinuated; a ridge or groove radiating from the beak to the lower posterior angle of the valves. Marine. Silurian to Trias.

Sanguinolites, M'Coy. Elongate, obliquely truncate behind; beaks low, sculpture of concentric or broken lines, anterior adductor scar buttressed by a ridge. Carboniferous.

Promacrus and *Prothyris*, Meek. Carboniferous.

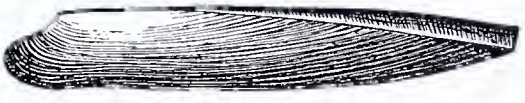


Fig. 600.

Solenopsis pelagica, Goldf. Devonian; Eifel District.

Arcomyopsis, Sandb. Somewhat curved, with prominent beaks; obliquely truncate behind; posterior area radially, the rest of the surface concentrically sculptured. Devonian.

Orthonota, Conrad; *Orthodesma*, Hall. Silurian.

Solenopsis, M'Coy (Fig. 600). Very long, scabbard-shaped, smooth; anteriorly short and rounded, gaping behind. Devonian to Trias.

Family 3. Vlastidae. Neumayr.

Shell thin, very inequivalve, beaks elevated, hinge line edentulous, arched, meeting at an obtuse angle beneath the beaks, leaving a dorsal opening; surface smooth or concentrically striate.

The two genera *Vlasta* and *Dux* (*Vevoda*), Barrande, from the Silurian of Bohemia (Etage E 2), constitute this family.

Family 4. Grammysiidae. Fischer.

Shell thin, equivalve, oval, or elongate, with the beaks sub-central to anterior; hinge edentulous, sometimes thickened. Ligament parivincular, external; pallial line not sinuate; surface smooth or concentrically sculptured. Silurian to Carboniferous.

[1] [The terms *Palaeoconcha*, *Taxodonta*, *Schizodonta*, etc., preceded by Roman numerals, are retained here merely as convenient descriptive appellations, and are in nowise to be regarded as possessing systematic values.]

Grammysia, Vern. (*Sphenomya*, Hall), (Fig. 601). Shell elongate-ovate, concentrically sculptured, with a deep lunule; cardinal margin thickened, edentulous; surface with several radial grooves. Silurian and Devonian. *Protomya*, Hall, is similar but without the grooves.

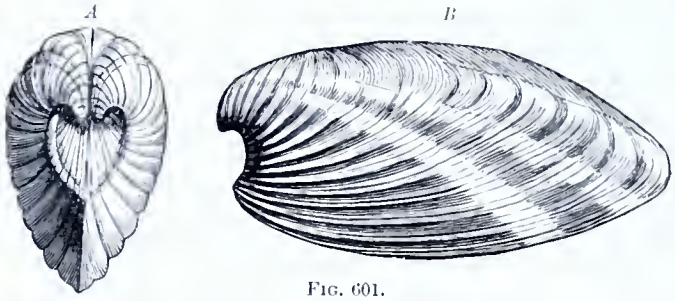


Fig. 601.

Grammysia Hamiltonensis, Vern. Spirifer Sandstone (Lower Devonian); Lahnstein, Nassau (after Sandberger).

Leptodomus, M'Coy, Silurian; *Elymella*, *Glossites*, *Euthydesma*, *Paleanatina*, and ? *Tellinopsis*, Hall; Devonian.

Cardiomorpha, de Kon. Oval, inflated, beaks almost anterior, conspicuous, adjacent, prosogyrous; hinge line thin, arched. Silurian and Carboniferous.

Isoculia, M'Coy. Like the preceding, but with coarse concentric sculpture. Carboniferous.

Other Carboniferous genera are *Broeckia*, de Kon.; *Chaenomya*, Meek; *Sedgwickia*, M'Coy; and *Edmondia*, de Kon. The last is like *Cardiomorpha*, but gapes in front, with a narrow ridge below the beaks.

The Cambrian *Fordilla*, Barrande, earliest of bivalves if a Mollusk, may possibly belong to the Crustaceans near *Estheria*. It is minute, oval, somewhat arcuate, and concentrically striated. Potsdam.

What appears to be a genuine Pelecypod, and so far the only one except *Fordilla* which is known from the Cambrian rocks, is *Modiolopsis priscus*, Walcott. It is transversely oval, with sub-central, incurved beaks, and an anterior adductor scar visible within an apparently simple pallial line. It is minute (2 mm. long), and known by an internal cast from the Lower Cambrian of Washington County, New York. The Ordovician *Redonia*, Rouault, is not dissimilar.

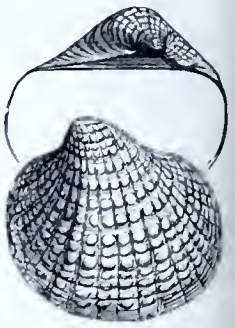


Fig. 602.

Cardiola cornucopiae, Goldf. Devonian; Ebersrenth, Fichtelgebirge. 1/1.

Family 5. **Cardiolidae**. Neumayr.

Shell equivalve, inflated, obliquely ovate, with prominent beaks, and edentulous hinge; sculpture often radial, or sometimes of concentric ridges, which may be confined to the beaks. Silurian and Devonian.

Cardiola, Brod. (Fig. 602): *Gloria*, Barrande; *Eopteria* (? *Euchasma*), Billings, from the Ordovician, may also belong here.

Family 6. **Antipleuridae**. Neumayr.

Shell very inequivalve, without gape below the beaks; hinge obscurely Taxodont, with an amplidetic area and predominantly radial sculpture. Silurian.

Antipleura, *Dualina*, and *Dalila* of Barrande.

Family 7. **Praecardiidae**. Neumayr.

Shell equivalve with Taxodont dentition and usually strong radial sculpture. Silurian and Devonian.

This family contains the following genera of Barrande from the Silurian of Bohemia:—*Praecardium*, *Paracardium*, *Puella*, *Pentata*, *Buchiola* (*Glyptocardia*, Hall), *Praelucina*, *Regina*, *Praelima*; to which Neumayr adds *Pleurodonta*, Conrath, and *Pararca*, Hall. It is possible that *Silurina*, Barrande, regarded by Neumayr as the

type of a distinct family, may also be included. It is distinguished by its feebler structure and a dorsal radial groove near the cardinal border.

II. Taxodonta. Neumayr (emend.)

Superfamily 1. NUCULACEA.

Shell of variable form, closed ventrally, equivalve, with a smooth epidermis; nacreous or porcellanous with tubuliferous external prismatic layer; area obscure, or none, when present divided into lunule and escutcheon; ligament variable, amphidetic; gills foliobranchiate; both adductors present and sub-equal; foot grooved and reptary, not byssiferous; marine.

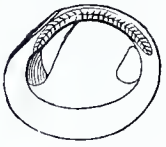


Fig. 603.

Ctenodonta pectunculoides, Hall. Ordovician; Cincinnati, Ohio. 2/1 (after Hall).

Family 8 ? Ctenodontidae. Dall.

Shell Nuculiform, with the teeth in a continuous arched series; no area; ligament external, alivincular, without an external resilium; pallial line simple. Ordovician and Silurian.

Ctenodonta, Salter (*Tellinomya*, Hall p.p.), (Fig. 603). Oval, smooth or concentrically striate, in the later horizons sometimes Ledaeform. Ordovician and Silurian.

Cuenullella (M'Coy), Fischer. Ovate, thin-shelled, with a straighter hinge line and a radial buttress to the anterior adductor. Silurian.

Family 9. Nuculidae. Adams.[1]

Shell compact, closed, with the teeth in two series meeting below the umbones, separated by a chondrophore; area represented by an obscure lunule and escutcheon; no ligament, but a wholly internal, amphidetic, alivincular resilium; internal layer of shell nacreous; mantle lobes free, without siphons; pallial line simple. Ordovician to Recent.

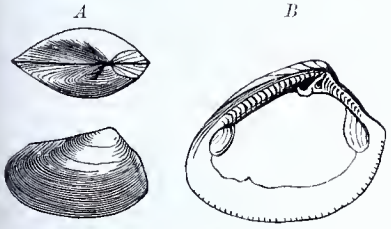


Fig. 604.

A, Nucula strigilata, Goldf. Upper Trias; St. Cassian, Tyrol. 1/1. *B, N. nucleus*, Linn. Miocene; Grussbach, near Vienna. 1/1.

Nucula, Lam. (*Nuculana*, Link), (Fig. 604). Oval or triangular, concentrically or reticulately sculptured. Silurian to Recent. Represented by over 200 fossil and half as many recent species.

Acila, Adams. With divaricate sculpture. Lower Cretaceous to Recent.

Family 10. Ledidae. Adams.[1]

Shell as in the Nuculidae, but elongated with the ligament variable, the resilium sometimes external or absent, the internal shell layer sub-nacreous or porcellanous, the ends of the shell partly gaping; the mantle lobes more or less united; with complete, sometimes elongate siphons; pallial line usually sinuated. Silurian to Recent.

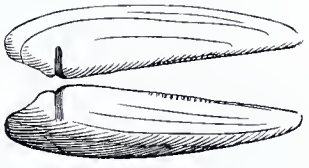


Fig. 605.

Cleidophorus cultratus, Sandb. Internal cast from Lower Devonian; Niederlahnstein, Nassau. 1/1.

Cleidophorus, Hall (*Adranaria*, Mun. Chalm.), (Fig. 605). Shell rostrate, the anterior side shorter, with an internal radial buttress. Silurian and Devonian.

Cytherodon, Hall. Silurian and Devonian. *? Redonia*, Rouault; *Cadomia*, Tromelin; *Tellinomya*, *Palaeoneilo*, Hall; *Anuseula*, Barr.; and *Myoplusia*, Neumayr. Silurian.

Leda, Schum. (Figs. 606, 607). Shell rostrate, elongate, often keeled, concentrically striate; hinge as in *Nuenla;* pallial sinus small. Silurian to Recent.

[1] *Verrill, A. E.*, and *Bush, K. J.*, Revision of the genera of Ledidae and Nuculidae (Amer. Journ. Science [4], vol. III. pp. 51-63), 1897.

Yoldia, Moller (Fig. 608). Shell thin, wide, and more or less gaping behind, hinge as in *Nucula*. Cretaceous to Recent.

Fig. 606.

Leda rostrata, Lam. sp. Middle Jura; Milhaud, Aveyron. 1/1.

Fig. 607.

Leda Deshayesiana, Duch. Oligocene; Rupelmonde, Belgium. 1/1.

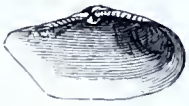


Fig. 608.

Yoldia arctica, Gray. Pleistocene; Bohuslan, Sweden. 1/1.

Fig. 609.

Nuculina ovalis, Wood sp. Miocene; Forchtenau, near Vienna.

Nuculina, d'Orb. (Fig. 609). Nuculiform, hinge teeth few and discrepant; with large lateral tooth and external ligament. Tertiary and Recent.

Malletia, Desm., and *Tindaria*, Bell. Yoldiform and Nuculiform respectively, but without internal chondrophore. Tertiary and Recent.

Superfamily 2. ARCACEA. Deshayes.

Shell of varied form, usually with a pilose epidermis, porcellanous, with tubuliferous non-prismatic external layer; area typically amphidetic, ligament external, ali- or multivincular; gills filibranchiate, with the filaments usually reflected; mantle lobes free, without siphons, the pallial line simple; foot variable, deeply grooved, byssogenous; marine or fluviatile.

Family 11. Parallelodontidae. Dall.

Shell Arciform, with the posterior hinge teeth elongated, tending to be parallel to the hinge margin; ligament multivincular. Carboniferous to Recent.

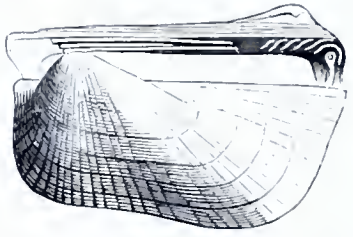


Fig. 610.

Parallelodon Hirsonensis, Morris and Lyc. Great Oolite; Minchinhampton, England. 1/1.

Fig. 611.

Cucullaea Hersilia, d'Orb. Oxfordian; Vieil St. Remy, Ardennes. 1/1.

The ancient forms of this group appear to connect with the *Pteriacea* through *Pterinea*, and with *Arca* through *Cucullaea*. The recent forms, which from their shell characters have been referred to *Macrodon*, are all small and abyssal. The relationship of this family to the *Arcidae* is very intimate but not exclusive.

Parallelodon, Meek (*Macrodon*, Lycett), (Fig. 610). Shell elongate, sub-quadrate, with amphidetic area, and prominent, rather anterior beaks. Anterior teeth transverse or flexuous, posterior long and parallel to the hinge line. Devonian to Tertiary; maximum in Coal Measures.

Grammatodon, Meek and Worthen, and *Nemodon*, Conrad, are allied. *Carbonarea*, Meek and Worthen. Beaks inflated, curved, angular behind ; hinge margin curved, with two oblique teeth. Carboniferous.

Cucullaea, Lam. (Fig. 611). Shell inflated, trapezoidal ; hinge teeth in the centre of the hinge short, transverse or oblique, the terminal teeth on each side longer, subparallel to the hinge line ; posterior adductor usually supported by a radial elevated lamina or buttress. Jura to Recent ; maximum in Mesozoic.

Cucullaria, Desh., of the Eocene, and *Idonearea*, Conrad, are closely allied.

Family 12. **Cyrtodontidae.** Ulrich.

Shell equivalve, short, usually heavy, convex, and earthy, without persistent epidermis, area small, ligament parivincular ? ; hinge teeth transitional between the Parallelodon and Dysodont type ; adductor scars sub-equal, the posterior larger but less impressed. Ordovician to Devonian.

These forms are evidently intermediate in character. They recall *Limopsis* among later types, are nearly related to the *Parallelodontidae*, but have not the multivincular ligament ; the hinge has Dysodont elements, but the difference of texture and epidermis stand in the way of assimilating them with the *Mytilacea*.

Cyrtodonta, Bill. (*Cyprieardites*, p.p. Conrad ; *Megalomus*, Hall). Shell rounded, moderately ventricose, with rather tumid, incurved, anterior beaks ; area narrow and obscure ; cardinal teeth two to four, obliquely curved or horizontal ; lateral teeth near the posterior end of the hinge elongate, strong, curved, or oblique ; pallial line simple. Anterior adductor set on the wall of the valve. Silurian.

Cypricardites, Conr. (*Palearea*, Hall). Five cardinal teeth present, the anterior largest. Silurian.

Vanuxemia, Bill. Beaks more nearly terminal, anterior adductor scar excavated out of the hinge plate. Ordovician.

Whitella, *Isehyrodonta*, Ulrich ; and *Matheria*, Bill. Silurian.

Family 13. **Limopsidae.** Dall.

Shell Pectunculoid, equivalve, or nearly so ; the ligament alivincular, partly immersed, its socket approaching a chondrophore ; area small ; foot long, narrow, grooved, byssiferous ; otherwise as in Arcidae. Trias to Recent.

These forms precede the typical *Arca* and have a special facies of their own. The two dental series of the hinge are often discrepant in character or direction, recalling the *Parallelodontidae*.

Limopsis, Sassi (Fig. 612). Small, rounded, or oval, recalling *Glycimeris*, except for the alivincular ligament. Trias to Recent.

Trinacria, Mayer (*Trigonocoelia*, Nyst). Like *Limopsis*, but triangular, with the posterior slope keeled. Eocene. *Cnisma*, Mayer, from the Eocene, appears to be related.

Fig. 612.

Limopsis aurita, Brocchi. Pliocene; Piacenza. 1/1.

Family 14. **Arcidae.** Dall.

Shell trapezoidal or rounded, with the posterior side longer ; ligament usually multivincular ; hinge typically Taxodont, with the teeth in two similar series, meeting below the beaks, and approximately vertical to the margin of the valve ; foot stout, short, deeply grooved. Jura to Recent.

Most of the Palaeozoic *Arca*-like forms are probably *Parallelodontidae*, and the typical Arcas are preceded by Pectunculoid forms. The convergence of the types of *Areacea* as we recede in geological time is very marked, and their relations to the *Nuculacea* are evident in spite of the later developed differences.

Arca, Lam. (type *A. Noae*, Lin.) Shell trapezoid, equivalve, with a wide amphidetic area, distant conspicuous beaks, and radial sculpture ; a wide byssal gape ; a long, straight, transversely dentate hinge line, with many small similar teeth. Tertiary and Recent. Used in the wider sense, to include all the groups of *Arcidae*, there are some 200 living and 300 to 400 fossil species.

Sub-genera : *Barbatia*, Gray (Fig. 613); *Scapharca*, *Noetia*, *Anadara* (Fig. 614), and *Argina*, Gray ; *Scaphula*, Benson (fresh-water), etc.

Isoarca, Münst. (Fig. 615). Shell smooth, inflated ; beaks full, incurved ; hinge line with rather amorphous dentition. Upper Jura and Lower Cretaceous.

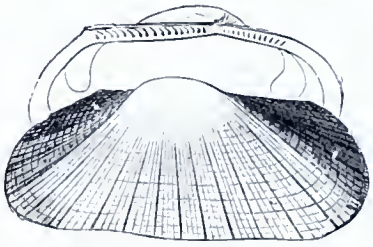


Fig. 613.

Arca (*Barbatia*) *barbata*, Linn. Miocene ; Grund, near Vienna. 1/1.

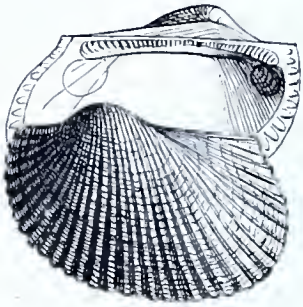


Fig. 614.

Arca (*Anadara*) *diluvii*, Lam. Pliocene ; Sienna.

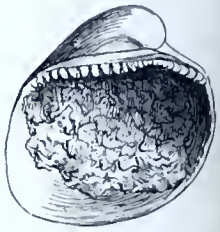


Fig. 615.

Arca (*Isoarca*) *cordiformis*, Ziet. Upper Jura ; Nattheim, Wurtemberg. 1/1.

Glycimeris, Da Costa (*Pectunculus*, Lam. *Axinea*, Poli), (Fig. 616). Rounded and almost symmetrical. Basal margin dentate ; area as in *Arca*, but shorter ; ligament

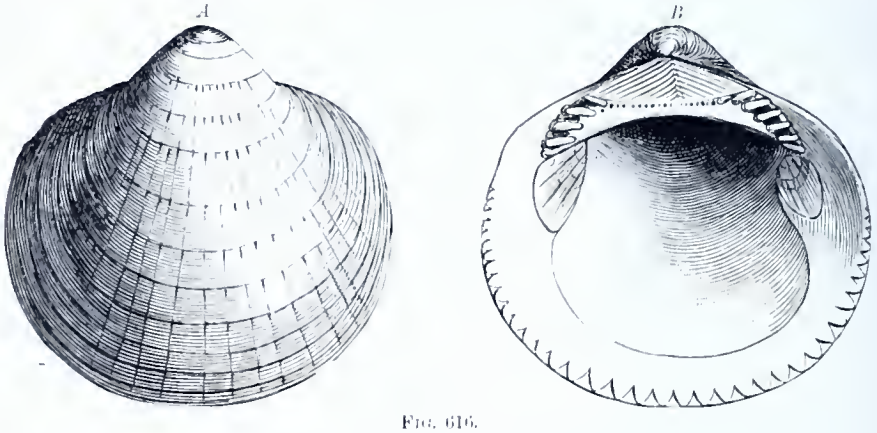


Fig. 616.

Glycimeris obovatus, Lam. Oligocene ; Weinheim, near Alzey. 1/1.

multivincular ; teeth oblique, in an arched series, interrupted during growth by the subsidence of the areal margin. Cretaceous to Recent ; maximum in Miocene.

III. Schizodonta. Steinmann (emend.)

Superfamily 3. PTERIACEA. Dall.

Shells of varied form, frequently alate, with a nacreous or sub-nacreous inner and prismatic outer layer ; the epidermis seldom conspicuous ; area amphidetic ; ligament variable, usually not parivincular ; gills filibranchiate or reticulate, usually reflected ; mantle lobes free, without siphons ; pallial line simple ; the anterior adductor smaller, or frequently

obsolete in the adult, though present in the young; generally byssiferous; hinge Schizodont or edentulous. The young sometimes showing a distinct nepionic stage. Marine.

Family 15. **Pterineidae.** Dall.

Shell Pteriiform, bialate, dimyarian, the anterior adductor smaller; inequivalve, very inequilateral; dentition obscure; ligament amphidetic, external, multivincular (?); the byssus passing through a notch in the smaller valve. Ordovician to Devonian.

In *Pterinea* and its allies we have the first indications of divergence of what ultimately became Taxodont and Schizodont dentition. From this assemblage, as indicated by Jackson, a large proportion of the *Prionodesmacea* have diverged in various directions. It is probable that from this source the filibranchiate Taxodonts have sprung, rather than directly from the foliobranchs.

Rhombopteria, Jackson (Fig. 617). Posterior wing separated from the body of the valve by a shallow sinus; anterior wing short; teeth obscure, the posterior elongated. Silurian.

Pterinea, Goldf. (Fig. 618). Left valve convex, right valve flat; hinge plate long, broad, auriculate before and behind; area amphidetic, grooved; ligament parivin-

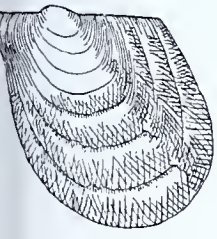


Fig. 617.

Rhombopteria mira, Barr. sp. Silurian (E); Prague (after Jackson).

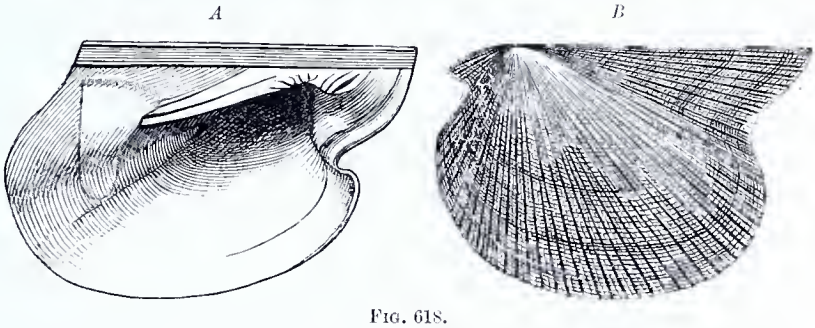


Fig. 618.

A, *Pterinea laevis*, Goldf. Devonian; Niederlahnstein, Nassau. Interior of left valve, 1/1. *B*, *P. lineata*, Goldf. Same locality; external view.

cular (?); anterior teeth obscure, transverse; the posterior elongate, nearly parallel to the cardinal margin, depressed behind. Posterior adductor scar large, the anterior small but strong, inserted below the anterior wing. Silurian to Carboniferous; particularly abundant in the Devonian of Europe and America.

Actinodesma, Sandb. (*Glyptodesma*, *Ectenodesma*, Hall; *Dolichopteron*, Maurer). Like *Pterinca*, but with the wings elongated and pointed. Devonian.

Leptodesma, Hall; *Kochia*, Frech (*Onychia*, Sandb.; *Loxopteria*, Frech). Devonian.

Family 16. **Lunulicardiidae.** Fischer.

Usually equivalve, triangular shells with terminal beaks, from which a sharp ridge runs toward the lower margin, bounding a flattened area. Hinge margin straight, long. Internal characters unknown. Silurian and Devonian.

Lunulicardium, Münst. Anterior side with a byssal sinus. Silurian and Devonian. *L. semistriatum*, Münst.

Patrocardium, Fischer (*Hemicardium*, Barr. non Cuvier). Without byssal sinus. Silurian.

Additional genera: *Amita* (*Spanila*, *Tetinka*), *Mila*, *Tenka*, *Babinka* (*Matercula*), Barrande. Silurian.

Family 17. **Ambonychiidae.** Miller.

Shell Mytiliform, with no anterior wing, the anterior adductor obsolete; equivalve, very inequilateral; dentition obsolete or Schizodont; ligament external, multivincular (?);

byssus passing through a narrow gape between the valves which are otherwise closed. Ordovician to Devonian.

The typical *Ambonychia*, according to Ulrich, is edentulous; the forms ordinarily passing under that name being now referred to *Byssonychia*. In this group the byssus does not pass through a notch in one of the valves.

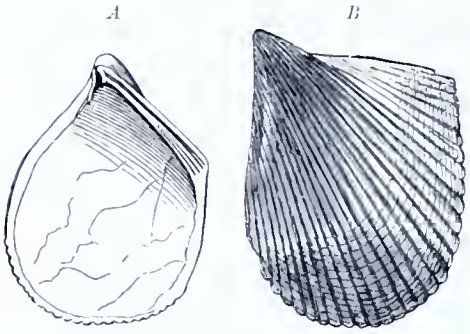


FIG. 619.

A, *Byssonychia*, sp. Cincinnati Group; Cincinnati, Ohio. Interior of right valve. 1/1 (after Miller). *B*, *B. radiata* (Hall), Ulrich. Same locality.

The *Ambonychiidae* include the typical members of *Ambonychia*, *Byssopteria*, and *Amphicoelia*, Hall; *Opisthoptera* (*Megaptera*), Meek; *Anomalodonta*, Miller; *Byssonychia* and *Allonychia*, Ulrich; and their allies.

Byssonychia, Ulrich (Fig. 619). Hinge with several small cardinal and two or three slender lateral teeth; area striated; otherwise as in *Ambonychia*.

Paleocardia, Hall. Silurian. *Mytilarca*, *Plethomytilus*, Hall. Devonian.

Gosseletia, Barrois (*Cyrtodontopsis*, Frech). Thicker shelled, with heavier and more numerous teeth. Devonian.

Clionychia, Ulrich. Edentulous, concentrically sculptured. Silurian.

Family 18. Pinnidae. Meek.

Shell Mytiliform, not alate, dimyarian, the anterior adductor smaller; equivalve,

FIG. 620.

Pinna pyramidalis, Münst. Quader Sandstein; Schandau. 1/3.

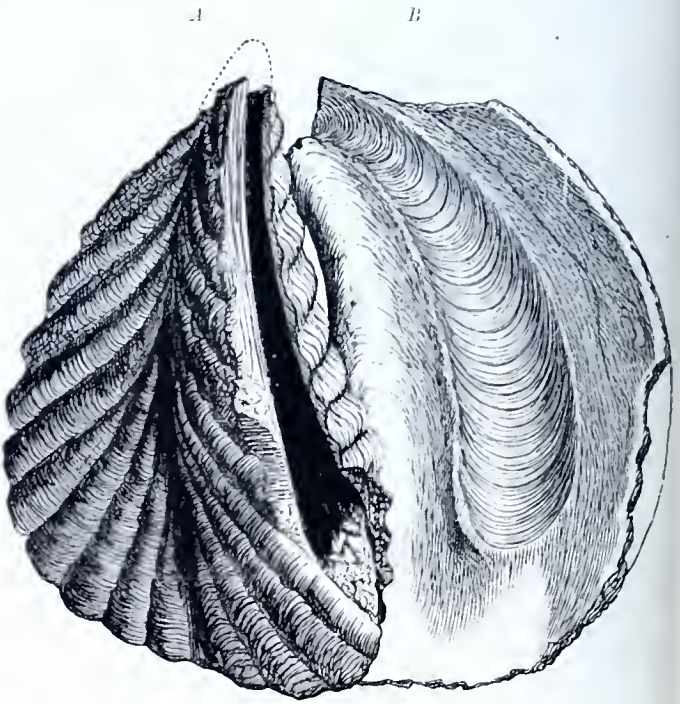


FIG. 621.

Pinnigena Seebachi, Böhm. Upper Jura; Kelheim, Bavaria. External and internal views, 1/3 natural size.

truncate, and wholly open behind; edentulous; area linear; ligament parivincular, in-

ternal; shell structure coarsely prismatic, with a thin, partial, nacreous lining; byssiferous. Devonian to Recent.

Palaeopinna, Hall. Devonian; North America.

Aviculopinna, Meek. A very small wing in front of the beaks. Carboniferous and Permian.

Pinna, Linn. (Fig. 620). Shell thin, with a long hinge line; valves carinate, triangular. Jura to Recent.

Pinnigena, Sauss. (*Trichites*, Plott), (Fig. 621). Muscular impression very large; prismatic layer extremely thick; sculpture divaricate. Jura and Cretaceous.

Atrina, Gray. Shell with broad adductor scars; short hinge line and entire nacreous layer. Carboniferous to Recent.

Cyrtopinna, Mörch. Jura to Recent.

Family 19. **Conocardiidae.** Neumayr.

Shell sub-trigonal, anteriorly truncate and gaping, the margins of the gape frequently produced into a tube-like rostrum and sharply serrate below, the posterior end usually alate, the wing divided internally by a longitudinal ridge; dimyarian, the anterior adductor scars smaller; equivalve more or less gaping behind; Schizodont, with a single anterior lateral, and an obscure or obsolete cardinal tubercle; area ill-defined, amphidetic; ligament external, parivincular; shell structure cancellate, or built up of hollow prisms resembling those of Pinna, but not solid; valves thick, internally marginate; byssiferous (?); marine. Silurian to Carboniferous.

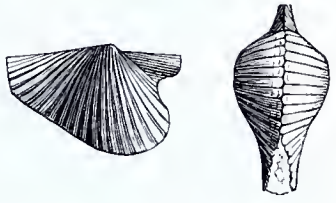


Fig. 622.

Conocardium alaeforme, Sow. Carboniferous Limestone: Tournay, Belgium. 1/1.

This group includes *Conocardium*, Bronn; (*Pleurorhynchus*, Phill.), (Fig. 622); and *Rhipidocardium*, Fischer. It is extremely isolated, and comprises some fifty species. These remarkable shells have been referred by most palaeontologists to the *Cardiacea*, with which they have no connection whatever except analogy of form with a few aberrant *Cardiidae*.

Family 20. **Pernidae.** Zittel.

Shell sub-mytiliform, with a broad posterior wing; monomyarian, the anterior adductor absent in the adult; inequivalve, teeth irregular or absent, with a serial multivincular ligament; byssiferous, with a moderate gape, or none. Permian to Recent.

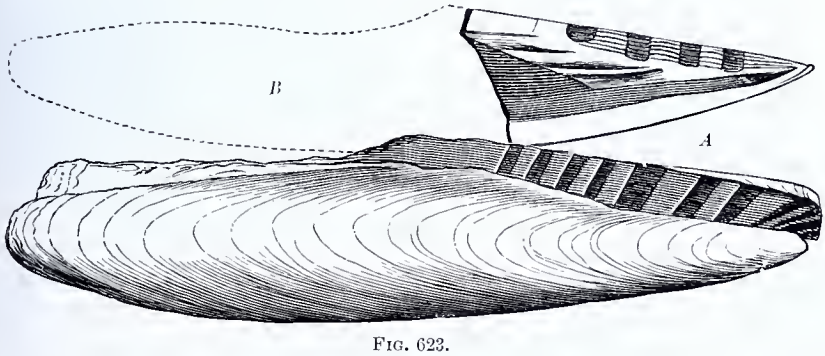


Fig. 623.

A, Gervillia aviculoides, Sow. Oxfordian; Dives, Calvados. *B, G. linearis*, Buvignier. Hinge.

This family differs from the *Pteriidae* chiefly by its multivincular ligament in the adult state. It finds its maximum development in the Jura and Cretaceous.

Bakewellia, King. Small, obliquely elongated, alate behind, three to four denticulations under the beaks. Permian.

Gervillia, Defr. (Fig. 623). Posterior wing obscure, hinge plate thick, beaks terminal, pointed, with obscure dental ridges sub-parallel to the long axis of the valve. Trias to Eocene.

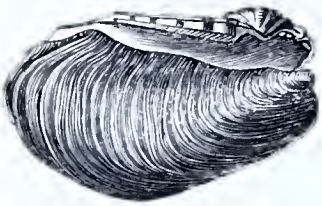


Fig. 624.

Hoernesia socialis, Schloth. sp. Muschelkalk; Würzburg, Bavaria.

Sub-genus *Hoernesia*, Laube (Fig. 624). With a strong tooth under the beak and sub-taxodont denticulations on the posterior cardinal border.

Odontoperna, Frech. Quadrate with two to three oblique dental folds below the beaks. Trias.

Perna, Brug. (*Isagnomon*, Klein; *Mulletia*, Fisch.), (Fig. 625). Equivalve, sub-quadrate, with terminal beaks, an anterior byssal notch, edentulous hinge, and numerous ligamentary grooves. Trias to Recent.

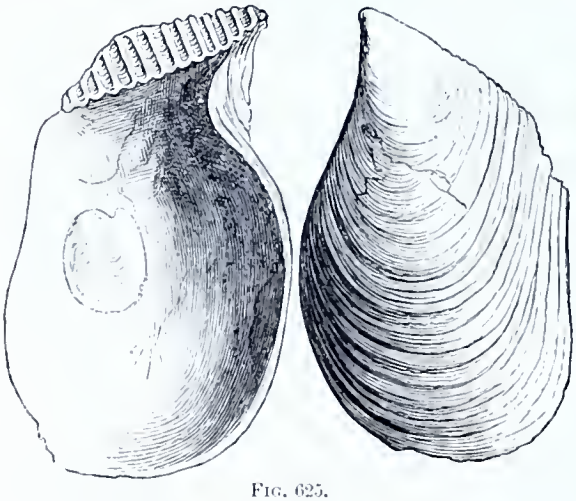


Fig. 625.

Perna Soldanii, Desh. Oligocene; Waldböckelheim, near Krenznach, Prussia. 1/2.

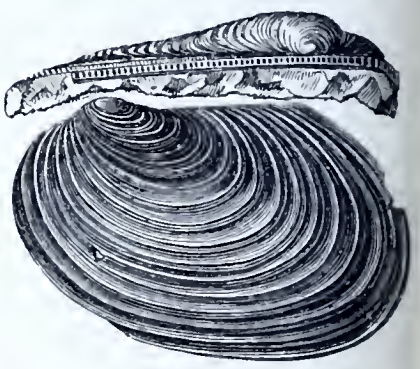


Fig. 626.

Inoceramus Cripsi, Mant. Upper Cretaceous; Gosau, Austria. 1/2 natural size.

Pernostrea, Munier-Chalmas. Jura.

Inoceramus, Sow. (*Catillus*, Brong.; *Haploscapha*, Conr.; *Neocatillus*, Fisch.), (Fig. 626). Rounded with concentric sculpture; prominent, rather anterior beaks, and edentulous hinge bearing numerous small ligamentary pits. Jura, and especially the upper and middle Cretaceous.

Sub-genera: *Actinoceramus*, Meek (Fig. 627), with radial sculpture; *Volviceramus*, Stol.; *Anopaea*, Eichw.

Fig. 627.

Actinoceramus sulcatus, Park. Gault; Perte du Rhône. 1/1.

Crenatula, Lam. Thin-shelled, elongate, smooth. Jura (?), Pliocene, and Recent.

Family 21. **Pteriidae**. Meek.[1]

Shell Aviculoid, bialate, monomyarian, inequivalve, with an alivincular ligament; the byssus issuing by a notch in the smaller valve; the young dimyarian, the anterior adductor disappearing with age. Silurian to Recent.

Pteria, Scopoli (*Avicula*, Brug.), (Fig. 628). Cardinal border in the young with pseudocardinal and lateral teeth, becoming more or less obscure with growth; shell thin, oblique. Devonian to Recent.

[1] *Bittner, A.*, Lamellibranchiaten der Alpinen Trias (Abhandl. k. geol. Reichsanstalt, Bd. XVIII.), 1895.

Sub-genera: *Actinopteria*, *Liropteria*, *Vertumnia*, Hall. Devonian. *Pteronites*, M'Coy. Devonian and Carboniferous. *? Rutotia*, de Kon. Carboniferous. *Oxytoma*, Meek (Fig. 629). Trias to Cretaceous. *Meleagrina*, Lam. Jura to Recent.

Limopteria, Hall (*Monopteria*, Meek; *Myalinodonta*, *Paropsis*, Oehlert). Anterior wing reduced, posterior large. Devonian and Carboniferous.

Pteroperna, Morris and Lycett. Middle Jura.

Fig. 628.

Pteria contorta, Portl. sp. Rhaetic; Kössen, Tyrol.

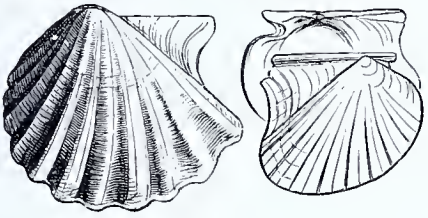


Fig. 629.

Pteria (*Oxytoma*) *costata*, Sow. Great Oolite; Luc, Calvados.

Fig. 630.

Pseudomonotis echinata, Sow. Cornbrash (Oolite); Sutton, England.

Pseudomonotis, Beyr. (*Eumicrotis*, Meek), (Fig. 630). Left valve flat, anterior wing not developed or minute. Devonian to Cretaceous.

Cassianella, Beyr. (Fig. 631). Left valve inflated with prominent incurved beak; the right flat or concave, without byssal sinus; teeth small as in *Pteria*, but more numerous; area amphidetic, wide. Trias.

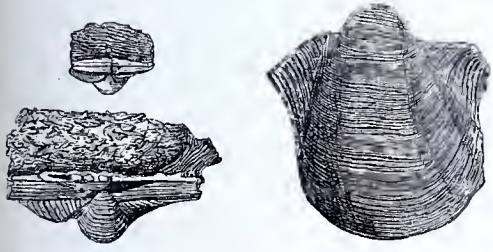


Fig. 631.

Cassianella gryphaeata, Münst. sp. Upper Trias; St. Cassian, Tyrol.

Fig. 632.

Monotis salinaria, Schloth. sp. Red Alpenkalk (Norian); Berchtesgaden, Bavaria. 2/3.

Monotis, Bronn (Fig. 632). Equivalve, compressed, radially striate, with low, sub-central beaks; anterior wing indistinct, rounded; posterior wing short, truncate or oblique. Trias.

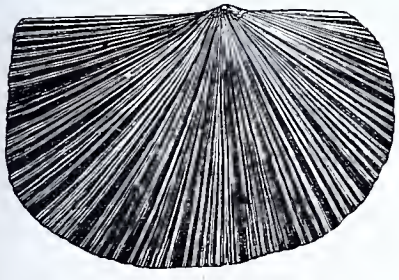


Fig. 633.

Halobia (*Daonella*) *Lommeli*, Wissm. Lower Keuper (Norian); Wengen, South Tyrol.

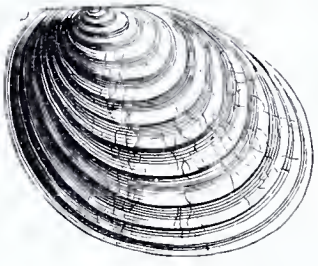


Fig. 634.

Posidonomya Becheri, Bronn. Culm Measures; Herborn, Nassau. 1/1.

Halobia, Bronn (*Daonella*, Mojs.), (Fig. 633). Equivalve like *Monotis*, but the anterior wing only represented by a smooth non-projecting area (*Halobia*), or both wings absent (*Daonella*). Abundant in the Trias.

Posidonomya, Bronn (*Ablacomya*, Steinm.), (Fig. 634). Equivalve, thin, compressed,

concentrically waved; hinge margin straight, edentulous; valves not auriculate; beaks sub-central, not conspicuous. Silurian to Jurassic. Over fifty species are known; very profuse in the Jura-Trias, sometimes forming massive beds.

Malleus, Lam.; *Philobrya*, Carpenter; *Hochstetteria*, Velain. Recent.

Family 22. **Myalinidae.** Frech.

Shell obliquely ovate, widened behind, sometimes with a small anterior ear; beaks anterior or terminal; hinge edentulous, straight; area amphidetic, longitudinally grooved; ligament parivincular? Adductor scars sub-equal; byssal notch distinct. Silurian to Jura.

Myalina, de Kon. Shell thick, oblique, with deep adductor scars anteriorly under the terminal beaks. Silurian and Devonian.

Hoplomytilus, Sandb.; *Myalinoptera*, Frech; *Ptychodesma*, *Mytilops*, *Modiella*, Hall. Devonian. *Leiomyalina*, Frech; *Aphanaia*, *Posidoniella*, de Kon.; *Liebea*, Waagen; *Atomodesma*, Beyr.; *Anthracoptera*, Salter. Carboniferous.

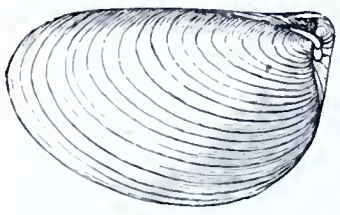


Fig. 635.

Aucella Mosquensis, Keys. Upper Jura; Moscow, Russia.

Pergamidea, Bitt. Thick-shelled, equivalve, inflated; anterior auricle distinct, sharply truncated; hinge margin notched below the beak. Trias of Asia Minor.

Mysidia, Bitt. Anterior ear reduced. Trias.

Aucella, Keys. (Fig. 635). Thin, inequivalve, inflated, small, concentrically waved, sometimes with radial striae. Left valve larger, arcuate, with very small anterior ear; right valve flatter and smaller. Area short, striated, with a ligamental sulcus below the beak. Upper Jura and Cretaceous; distribution world wide.

Family 23. **Vulsellidae.** Adams.

Shell Ostreiform, not alate, monomyarian, edentulous, inequivalve, with an alivincular ligament; byssus wanting; otherwise as in the Pteriidae. Tertiary to Recent. A degraded type which has become specialised through commensalism with Sponges.

Vulsella, Lam. (Fig. 636). Shell vertically produced, irregular, edentulous, with a triangular chondrophore for the ligament. Eocene to Recent.

Vulsellina, de Raine. Eocene. *? Chalmasia*, Stol. Cretaceous. (*? Ostreidae.*)

Fig. 636.

Vulsella Caillaudi, Zitt. Lower Eocene; Minich, Egypt. 2/3.

Superfamily 4. **OSTRACEA.** Goldfuss.

Shell degenerate, sessile, inequivalve, generally edentulous, wings obsolete; with a sub-nacreous or porcellanous inner and prismatic outer layer; epidermis inconspicuous; area amphidetic, ligament alivincular; foot and byssus absent; valves usually close-fitting; mantle lobes free, without siphons.

Family 24. **Ostreidae.** Lamarck.

Shell distorted by early adherence to other objects; monomyarian, the anterior adductor absent; edentulous, or with obscure Schizodont dentition; dimyarian when young; the foot obsolete or absent in the adult. Carboniferous to Recent.

Ostrea, Linn. (Fig. 637). Shell irregular, inequivalve, and with terminal beaks, with radial or foliaceous sculpture, usually discrepant on the two valves. Some

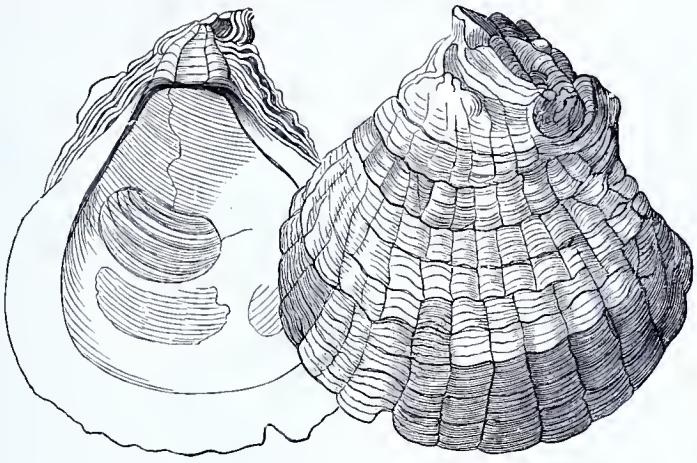


Fig. 637.
Ostrea digitalina, Dubois. Miocene; Vienna Basin.

species (*O. virginica*, *O. titan*, *O. gigantea*, etc.) attain a very large size. Carboniferous to Recent.

Alectryonia, Fischer (*Dendrostrea*, Swains.; *Actinostreon*, Bayle), (Fig. 638). Left valve attached to roots or branches by clasping shelly processes; both valves with

Fig. 638.
Alectryonia gregaria, Sow. sp. Oxfordian; Dives, Calvados.

Fig. 639.
Gryphaea arcuata, Lam. Lower Lias; Pfohren, near Donaueschingen, Baden.

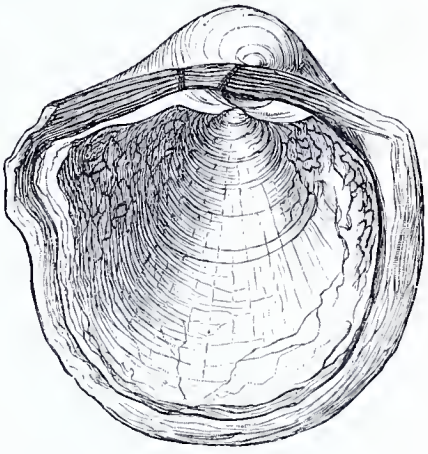


Fig. 640.
Gryphaea vesicularis, Lam. White Chalk; Isle of Rügen.

strong, often divaricate folds and undulate margins. Trias to Recent; maximum in Jura and Cretaceous.

Gryphaea, Lam. (*Pycnodonta*, Fisch.; *Gryphaeostrea*, Conr.), (Figs. 639, 640). Left valve strongly arched, with incurved beak, sessile when young, later free; right valve flat and opercular. Lias to Tertiary; chiefly Mesozoic.

Exogyra, Say (*Amphidonta*, Fischer; *Ceratostreon*, *Aetostreon*, *Rhynchostreon*, Bayle), (Figs. 641, 642). Resembling *Gryphaea*, but the valves more equal, hinge with an obscure tooth, beaks of both valves more or less spiral, the pit for the ligament narrow. Upper Jura and Cretaceous.

Terquemia, Tate (*Carpenteria*, Desl.) Shell with a marginal ridge, sessile by the right valve; left valve flatter, free. Trias and Lias.

Fig. 641.

Exogyra columba, Lam. Greensand (Cenomanian); Regensburg, Bavaria.

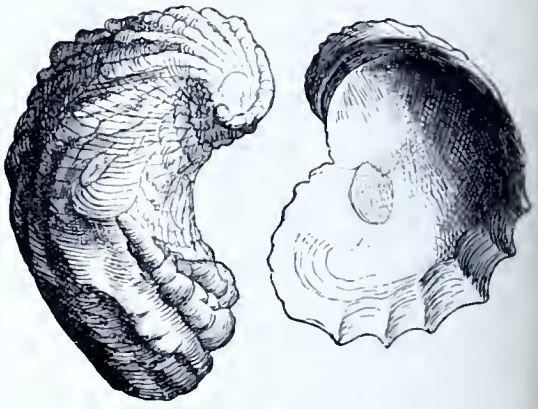


Fig. 642.

Exogyra flabellata, Goldf. sp. Cenomanian; Saint Paul Cloister, Egypt.

Family 25. **Eligmidae.** Gill.

Shell thick, sub-equivalve, free when adult, resembling Chalmasia in form, anteriorly with an irregular pedal gape; edentulous, monomyarian, with the adductor seated on the free extremity of a myophore projecting from the umbonal cavity, otherwise like the Ostreidae. Upper Jura.

Eligmus, Desl. If the characters of this genus have been correctly interpreted, it can hardly be retained in the *Ostreidae*. Further investigation of the genus is desirable.

Superfamily 5. NAIADACEA. Menke.

Shell of varied form, normally equivalve, inequilateral, and dimyarian; rarely alate; shell substance nacreous and prismatic, with a conspicuous epidermis; area obscure or amphidetic; ligament parivincular, usually opisthodetic and external; pallial lobes usually free, except for an anal siphon, the pallial line simple; foot normally long, compressed, keeled; byssus obsolete; young usually with a distinct nepionic stage; station usually fluviatile or lacustrine.

Family 26. **Cardiniidae.** Zittel.

Shell equivalve, closed, with feeble concentric sculpture or smooth; dentition Schizodont or obscure; ligament opisthodetic, external; dimyarian, adductor scars sub-equal, pedal scars feeble or invisible; station marine or brackish water. Devonian to Trias.

Amnigenia, Hall. Devonian (Catskill) of North America, and Rhenish Prussia.

Anthracosia, King (Fig. 643). Shell thin, oblong; hinge with a blunt elongated cardinal, and a feeble posterior lateral tooth upon a thickened hinge plate. Common in the Coal Measures and estuarine Permian of Russia.

Anthracomya, Salter; *Nayadites*, Dawson; *Asthenodonta*, Whiteaves; *Carbonicola*, M'Coy. Coal Measures. *Palaeomutela* and *Oligodon*, Amalitzky. Brackish Permian marls of Russia.

Anoplophora (Sandb.), Koenen (*Uniona*, Pohlig), (Fig. 644). Right valve with a blunt thick cardinal tooth fitting into a socket in the opposite valve. Left valve beside the socket has a long posterior lateral tooth. Trias (Lettenkohle). *A. donacina*, Schloth.; *A. lettica*, Quenst.

Trigonodus, Sandb. (Fig. 645). Cardinal tooth strong, triangular, sometimes divided, short, oblique, anterior; two elongate laterals in the left valves, and one

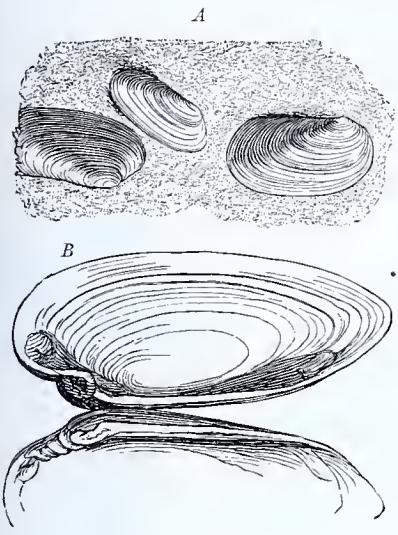


Fig. 643.

A, *Anthracosia carbonaria*, Goldf. sp. Permian; Niederstaufenbach, near Kusel, Rhenish Bavaria. *B*, *A. Lottneri*, Ludw. sp. Coal Measures; Hannibalzeche, near Bochum, Westphalia (after Ludwig).

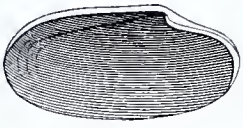


Fig. 644.

Anoplophora lettica, Quenst. sp. Trias; Friedrichshall (after Alberti).

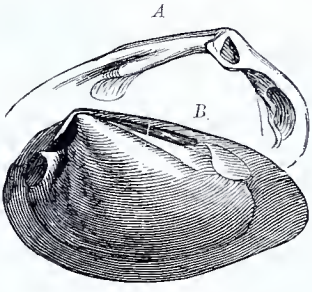


Fig. 645.

Trigonodus Sandbergeri, Alberti. Trias (Lettenkohle); Zimmern, Wurtemberg. *A*, Hinge, from a reverse impression of cast. *B*, Natural cast. $^1/_1$.

lateral in the right valve. Trias; especially common in the Lettenkohle dolomite and the Raibl beds.

Heminajas, Neumayr. Trias. *H.* (*Myophoria*) *fissidentata*, Wöhrmann.

Pachycardia, Hauer. Oblong or trigonal, concentrically striate or smooth; beaks nearly terminal, curved, adjacent, with a lunule; anterior end inflated, blunt;

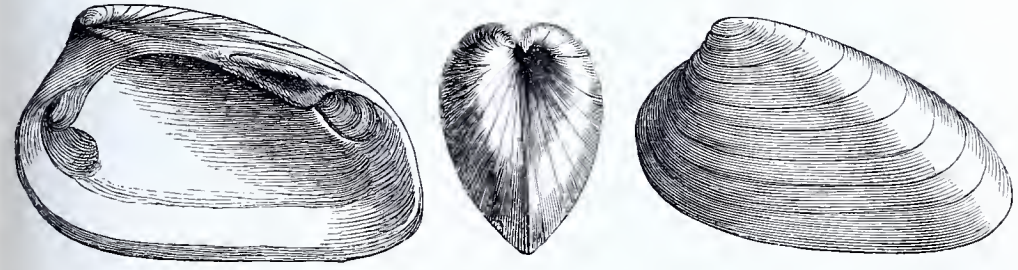


Fig. 646.

Cardinia hybrida, Sow. Lower Lias; Ohrsleben, near Halberstadt, Saxony.

posterior compressed; two strong divergent cardinal teeth in each valve, the anterior on the right being weaker and nearly marginal; each valve has also a long posterior lateral tooth. Alpine Trias.

Cardinia, Agassiz (*Thalassites*, Quenst.), (Fig. 646). Oblong, thick, short anteriorly, rounded. Cardinal teeth weak or obsolete, posterior lateral strong. Lower Lias, and reported also from the Dogger.

? *Nyassa*, Hall. Devonian. ? *Guerángeria* (*Davousti*), Oehlert. Lower Devonian.

Family 27. **Megalodontidae.** Zittel.

Shells equivalve, sub-Mytiliform, closed, with feeble concentric sculpture or none; dimyarian, with amphidetic area, and external opisthodetic ligament, frequently supported by nymphae; cardinal teeth strong, usually two or three, with a posterior lateral, all heavy and amorphous; anterior adductor scars distinct, with a well-marked myophoric ridge and pedal scar, the posterior adductor scars frequently bordered by an elevated crest. Marine. Devonian to Cretaceous.

These shells, which are often very ponderous, sometimes bear a remarkable resemblance to some recent American Unionidae. The myophoric ridge is common to very distinct bivalves of many unrelated groups. The true position of these forms cannot be regarded as positively fixed as yet.

Megalodon, Sow. (*Taurocerus*, *Lycodes*, Schafh.; *Conchodon*, Stopp.), (Figs. 647-649). Beaks prosogyrous; hinge plate very broad and massive, without laterals; the two cardinal teeth separated by a deep socket; anterior adductor scar small, semilunar,

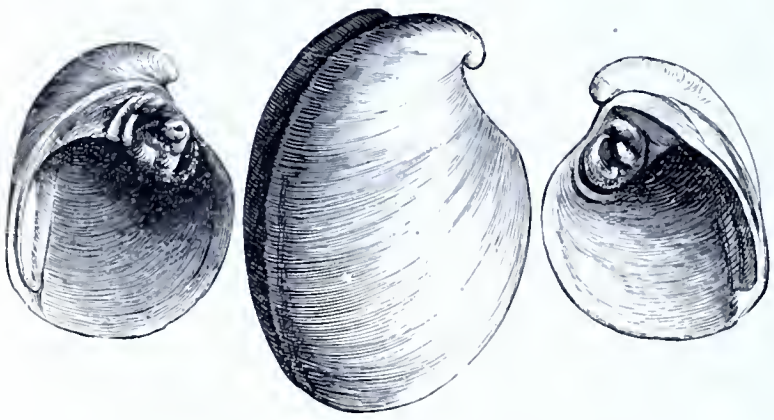


FIG. 647.

Megalodon (*Eumegalodon*) *cucullatus*, Goldf. Devonian; Paffrath, near Cologne. 1/1.

FIG. 648.

Megalodon (*Neomegalodon*) *triqueter*, Wulfen sp. Internal cast. Trias dolomite; Bleiberg, Carinthia.

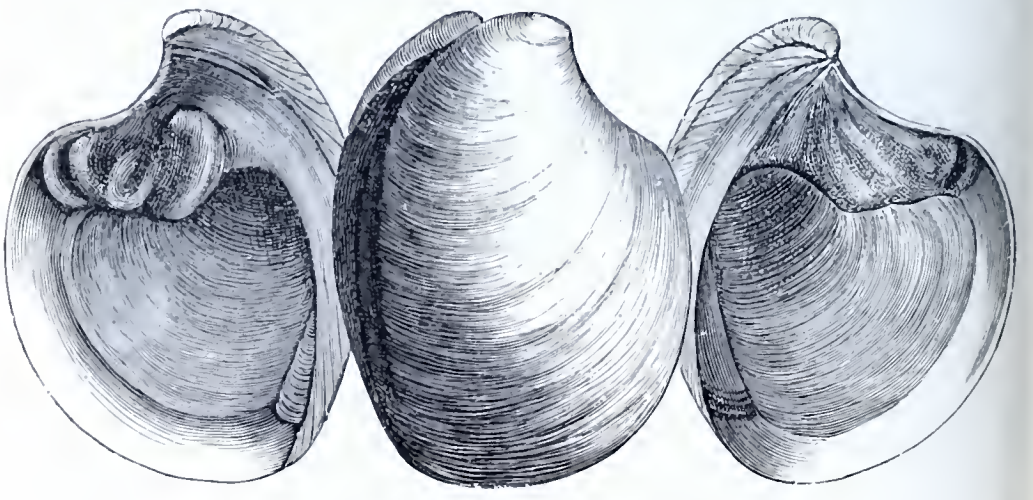


FIG. 649.

Megalodon (*Neomegalodon*) *Gümbeli*, Stoppani. Rhaetic; Elbigenalp, Tyrol (after Gümbel).

in front of the anterior cardinal; posterior scar longer, less distinct, situated on an elevated or thickened radial ridge. The oldest Devonian species (*M. cucullatus*, Goldf.) has amorphous cardinals and a smooth rounded shell (*Eumegalodon*). The Triassic species sometimes attain a large size, have a radial posterior ridge, smooth teeth, and divided right posterior cardinal teeth (*Neomegalodon*, Gümb.) They are extraordinarily abundant in the Dachstein, Limestone, and Hauptdolomite of the Northern Alps, and are also plentiful in the Raibl and Rhaetic beds of the Southern Alps.[1]

Pachyrisma, Morr. and Lyc. (*Pachymegalodon*, Gümb.) Like *Megalodon*, but with a larger anterior adductor scar, a rounded anterior tooth before the cardinals, and a strong posterior lateral. Trias to Upper Jura.

Durga, Böhm. Like *Pachyrisma*, but without an elevated area at the posterior adductor. Lias.

Protodiceras, Böhm. Lias. *Dicerocardium*, Stoppani. Rhaetic.

Family 28. **Unionidae**. Fleming.

Shell equivalve, dimyarian, typically Schizodont, with pseudocardinals and laterals if dentiferous; conspicuously nacreous; beaks usually sculptured; ligament opisthodetic, external; lobes of the mantle united to form an anal siphon, but the functional branchial siphon usually incomplete below; foot compressed, keeled, large, rarely with a feeble byssus; usually dioecious; the young having a distinct nepionic stage (glochidium). Fluviatile. Trias to Recent.

Typical Uniones make their appearance in the Trias of Texas, but are not abundant until the Cretaceous and Tertiary. The origin of the family has been sought in the *Trigoniidae*,[2] which have a very similar ontogeny as a group; in *Trigonodus*[3] and related forms; and by Pohlig in the Triassic *Uniona*. An older view recognises the Carboniferous *Anthracosia* and other *Cardiniidae* as probable ancestors. The weight of evidence is in favour of the latter, though there is much probability that each of these groups bears a certain amount of relationship to the present family, which will be better realised when more evidence is obtainable.

Unio, Retzius (Fig. 650). This, the typical genus, was founded on the pearl mussel (*Mya margaritifera*, Linn.), in which the posterior laminae of the hinge are

FIG. 650.

Unio Stachei, Neumayr. Pliocene (Congerian stage); Sibinj, Slavonia. *p*, Adductor; *x*, Pedal scar.

obsolete. The majority of species, however, have amorphous, heavy, radial, pseudocardinal and lateral teeth on the hinge; the shell is variable in form and ornamentation, some species having strongly marked sexual differences in the shell. Most of the species are pearly, with a conspicuous brown or greenish periostracum; the anterior adductor scars are high, and the pedal scars conspicuous.

[1] *Tausch, L. von*, Ueber Conchodus, etc. (Abhandl. geol. Reichsanstalt, XVII.), 1892.

[2] *Neumayr, M.*, Ueber die Herkunft der Unioniden (Sitzber. Wien. Akad. XCVIII.), 1889.

[3] *Wöhrmann, S. von*, Ueber die systematische Stellung der Trigonidem und die Abstammung der Nayaden (Jahrb. geol. Reichsanst. Bd. XLIII.), 1893.

Anodonta, Cuv. Valves thin, and armature of the hinge obsolete; lives in still, muddy water. Tertiary and Recent.

Family 29. **Mutelidae.** Gray.

Shell and anatomy resembling the Unionidae, without pseudocardinals and laterals; having, when dentiferous, an irregularly Taxodont hinge armature, generally partly closed mantle lobes, a complete branchial septum, more complete siphons, and with a nepionic stage represented by a Lasidium, resulting in unsculptured beaks for the adult shell. Cretaceous to Recent.

Spatha, Lea. Elongated, inequilateral, with a short edentulous hinge. Upper Cretaceous of Provence, and Recent in South Africa.

Leila, Gray; *Aplodon* and *Plagiodon*, Spix; *Mycetopus*, d'Orb.; *Mutela*, Scopoli; and *Iridina*, Lam. Recent.

Family 30. **Etheriidae.** Lamarck.

Shell sessile, irregularly modified by adherence to other bodies, nacreous, with a tendency to cellularity of structure; edentulous; ligament amphidetic, parivincular, deeply sunken, with a large internal resilium, modified by the distortion of the valves; young regular, equivalve, dimyarian; the adult irregular, inequivalve, and either (1) *monomyarian, or* (2) *with a very degenerate anterior adductor, or* (3) *with sub-equal adductors. Mantle lobes united only for the anal siphon; foot degenerate or absent in the adult; young byssiferous; station fluviatile.* Pleistocene and Recent.

The young shell of *Bartlettia* has well-marked nymphae and internal resilium. The relationship of the Naiades to *Pteria* renders the remarkable resemblance of the adult *Mulleria* to *Ostrea* less surprising, since *Ostrea* is now known also to be derived from the *Pteriidae*.

Etheria, Lam. Ostreiform, attached to rocks in African rivers. Also Pleistocene of West Africa.

Mulleria, Ferussac; *Bartlettia*, Adams. Recent; South American rivers.

Superfamily 6. **TRIGONIACEA.** Bronn.

Shell equivalve, inequilateral, closed, dimyarian, not alate; shell substance nacreous and prismatic; hinge teeth few, sub-umbonal, typically Schizodont; area obscure or none; ligament parivincular, opisthodetic, external; gills filibranchiate; mantle lobes usually free, but modified on the posterior edges to form functional siphons without conjunctive partitions; pallial line usually simple; non-byssiferous, though possessing an obsolete byssal apparatus; young without a distinct nepionic stage; dioecious; marine.

Family 31. **Lyrodesmidae.** Ulrich.

Shell with the hinge armature radiating fan-like from below the umbones; teeth five to nine; pallial line feebly sinuate or simple. Silurian.

Lyrodesma, Conr. (*? Actinodonta*, Phil.) Shell oval, cardinal border narrow, without ligamentary area. Silurian; America and Europe.

Family 32. **Trigoniidae.** Lamarck.

Shell with few hinge teeth ($\frac{2}{3}$), *the mantle lobes wholly free, but so applied to each other in life as to form functional siphons; pallial line simple.* Devonian to Recent.

Schizodus, King (Fig. 651). Ovate or quadrate, smooth; lateral teeth not fluted; anterior adductor scar with a small radial buttress. Abundant in the Permian.

Myophoria, Bronn (*Neoschizodus*, Gieb.), (Figs. 652, 653). Smooth or radially sculptured, usually with a strong radial ridge extending from the umbones backward and downward to the basal margin; the sculpture on the areas thus separated usually discrepant. Beaks mesogyrate,

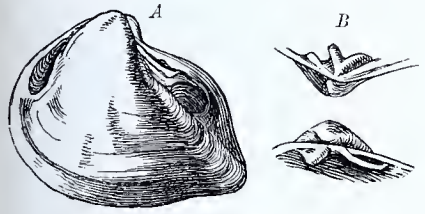


Fig. 651.

Schizodus obscurus, Sow. Zechstein; Niederrodenbach, near Hanau. *A*, Cast, 1/1. *B*, Hinge, 1/1 (after King).

Fig. 652.

Myophoria laevigata, Alb. sp. Schaumkalk; Rüdersdorf, near Berlin. 1/1.

Fig. 653.

Myophoria decussata, Münst. Upper Trias; St. Cassian, Tyrol. *A*, Exterior of right valve, 1/1. *B*, Enlarged view of hinge.

lateral teeth fluted, muscular scars buttressed by feeble ridges. Abundant in the Trias.

Sub-genus: *Myophoriopsis*, Wöhrmann.

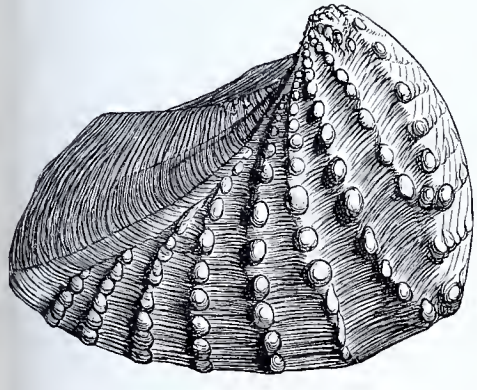


Fig. 654.

Trigonia navis, Lam. Lower Brown Jura; Gundershofen, Alsace. 1/1.

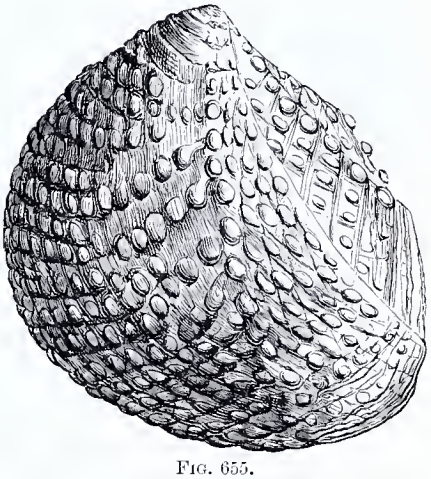


Fig. 655.

Trigonia daedala, Park. Middle Cretaceous (Hervien); Meule de Bracquegnies, Belgium. 1/1.

Trigonia, Brug. (Figs. 654-658). Surface sculptured with nodulose ribs or rows of

Fig. 656.

Trigonia costata, Sow. Middle Jura; Wurtemberg. 1/2.

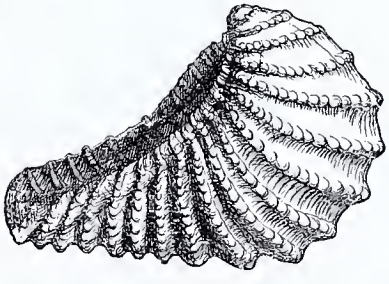


Fig. 657.

Trigonia, cf. *aliformis*, Park. Senonian; Vaels, near Aix-la-Chapelle. 1/1.

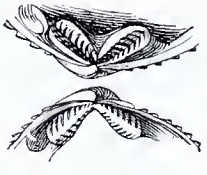


Fig. 658.

Trigonia pectinata, Lam. Recent; Australia. Hinge, 1/1.

pustules, the posterior dorsal area usually discrepant with the rest. Beaks opistho-

gyrous, nearly terminal; teeth striated; adductor scars strong, with buttressing ridges. Lias to Recent; abundant in Jura and Cretaceous, very sparse in later horizons.

IV. Isodonta. Fischer.

Superfamily 7. PECTINACEA. Reeve.

Shell usually inequivalve, flabelliform, more or less auriculate, and monomyarian; shell structure sub-nacreous, corrugated, and rarely prismatic, occasionally tubular; area, when present, amphidetic; ligament amphidetic, alivincular; gills filibranchiate, free, the filaments with or without a reflected limb; mantle lobes free, without siphons, usually with ocelli, papillae, or other tactile prominences along the margin, and with an inner projecting lamina (curtain) near the margin, at right angles to the plane of the valves; pallial line simple; foot small, usually sub-cylindrical, grooved, and byssiferous; usually monoecious; marine.

Family 33. Pectinidae. Lamarck.

Shell inequivalve, inequilateral, auriculate, usually closed, monomyarian, usually free; area amphidetic or obscure; ligament obsolete externally, the immersed portion forming an internal resilium, provinculum Taxodont in the very young, obsolete later, the crural teeth feeble or not developed. Silurian to Recent.

Fig. 659.

Aviculopecten papyraceus, Sow. Coal Measures; Werden, Westphalia.

Aviculopecten, M'Coy (Fig. 659). Shell Pectiniform, radially sculptured. Hinge margin long, feebly auriculate; ligament in numerous shallow grooves radiating to the amphidetic margin of the area. Silurian to Carboniferous.

Sub-genera: *Pterincopecten*, Hall; *Orbipecten*, Frech (*Lyriopecten*, Hall). Devonian.

Crenipecten, Hall (*Pernopecten*, Winch.) Like *Aviculopecten*, but with a Taxodont hinge. Carboniferous.

The preceding genera lead up to the prototypes of *Pteriidae* as a radical for the present family.

Pecten, Müller (*Vola*, Mörch; *Janira*, Schum.; *Neithea*, Drouët), (Fig. 660). Shell nearly equilateral, very inequivalve, sub-symmetrical, with well-developed, sub-equal ears; one valve (usually the right) more convex than the other; interior of the valves not lirate; hinge with a strong medial internal resilium, on each side of which interlocking crural ridges and grooves radiate in the adult; byssal notch inconspicuous. Cretaceous to Recent.

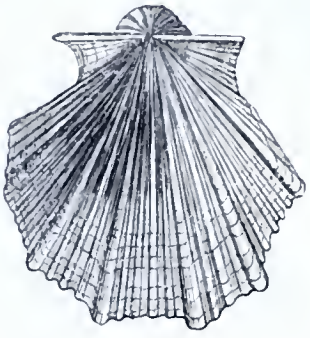


Fig. 660.

Pecten quinquecostata, Sow. Cenomanian; Rouen. 1/1.

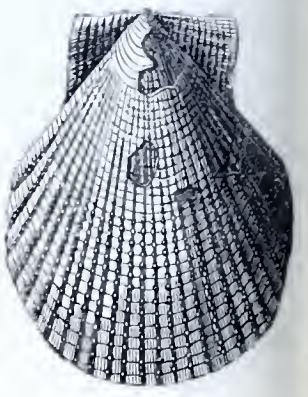


Fig. 661.

Pecten (*Chlamys*) *subtextorius*, Goldf. Coral-Rag; Nattheim.

The above diagnosis is of the sub-genus *Pecten* s. s. In a wide sense all the species of *Pecten* are free and auriculate, and without internal lirae. They have been divided into an excessive number of sections according to the superficial shell characters, but these rarely march with anatomical differences, and

cannot properly be regarded as of generic value. The most familiar of the groups thus named are as follows :—

Chlamys, Bolten (*Pallium*, Schum. ; *Decadopecten*, Rüpp.), (Figs. 661, 662). Shell

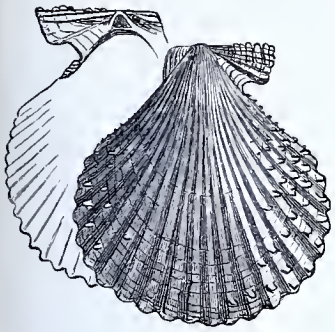


Fig. 662.

Pecten (*Chlamys*) *varius*, Linn. Pliocene ; Rhodes.

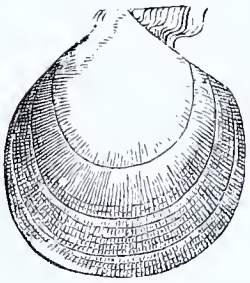


Fig. 663.

Pecten (*Camptonectes*) *lens*, Sow. Middle Jura ; Balin, near Cracow. 1/1.

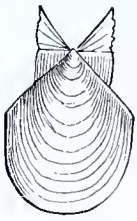


Fig. 664.

P. (*Entolium*) *cornutus*, Quenst. Upper Jura ; Hohenzollern. 1/1.

radially sculptured, nearly equivalve, with small, unequal ears, and deep byssal notch with well-developed etenolium. Trias to Recent.

Camptonectes, Ag. (Fig. 663). Shell small, thin, nearly smooth, with fine divergent striation radiating from a median line. Jura to Recent.

Entolium, Meek (Fig. 664). Smooth, thin, with sub-equal ears diverging at a sharp angle above the beaks ; byssal notch obsolete. Carboniferous to Cretaceous.

Pseudamusium, Adams. Shell small, thin, glassy ; the posterior ear obsolete, byssal notch distinct. Cretaceous to Recent. *Syncyclonema*, Meek is scarcely different.

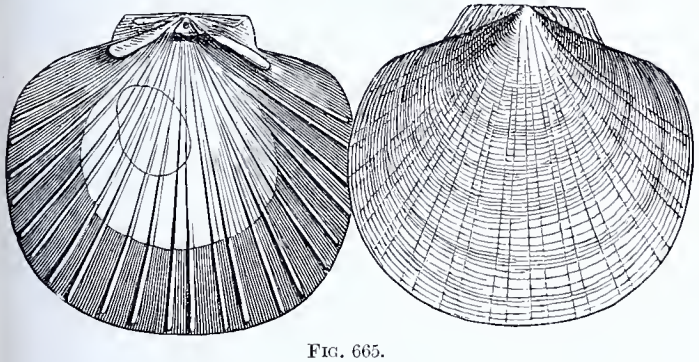


Fig. 665.

Amusium cristatus, Bronn sp. Miocene ; Baden, near Vienna. 1/1.

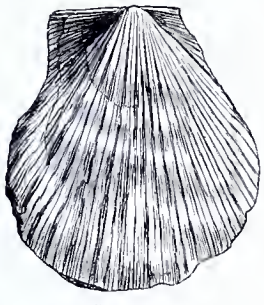


Fig. 666.

Hinnites abjectus, Phill. sp. Middle Jura ; Balin, near Cracow. 1/1.

Amusium, Schum. (Fig. 665). Shell with raised radial riblets internally ; externally smooth or delicately sculptured ; valves large, flattish, with sub-equal ears ; byssal notch inconspicuous or absent. Lias to Recent.

Sub-genus : *Propeamusium*, Greg. Small, thin, abyssal ; often with relatively conspicuous sculpture, usually discrepant on the valves. Tertiary and Recent.

Hinnites, Defr. (Fig. 666). Shell free and Pectiniform when young, later adherent to other objects and more or less distorted. Trias to Recent.

Pedum, Brug. Shell with an alivincular ligament in an open groove and area like that of *Spondylus* in the adult ; the young like *Chlamys*. Recent ; sessile in corals.

Family 34. **Spondylidae.** Fleming.

Shell inequivalve, nearly equilateral, closed, Pectiniform, obscurely auriculate, monomyarian ; sessile ; area amphidetic, much larger on the attached valve ; ligament alivincular, resilium more or less submerged ; byssus obsolete ; hinge with a Taxodont provinculum,

becoming obsolete in the adult and replaced by the typically Isodont development of the crura; otherwise as in the Pectinidae. Trias to Recent.

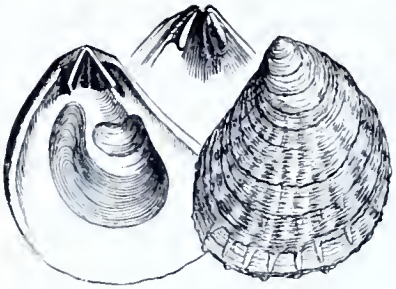


Fig. 667.

Plicatula pectinoides, Lam. Middle Lias; Nancy, France.

Plicatula, Lam. (*Harpax*, Park), (Fig. 667). Shell compressed, with coarse radial, often divaricate ribbing, a small area, and long shallow crenulate crural teeth, diverging at a sharp angle. Trias to Recent; maximum in Jura and Cretaceous.

Spondylus, Linn. (Figs. 668, 669). Shell inflated, with radial, often spiny or foliaceous sculpture; attached valve with a conspicuous area; crural teeth heavy, short, smooth. Jura to Recent; maximum from the Tertiary onward.

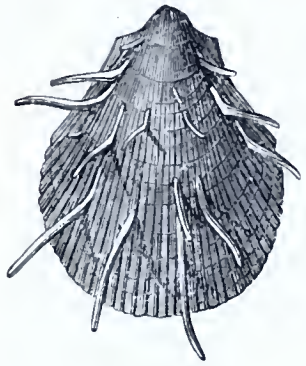


Fig. 668.

Spondylus spinosus, Sow. sp. Planerkalk; Strehlen, near Dresden. 2/3.

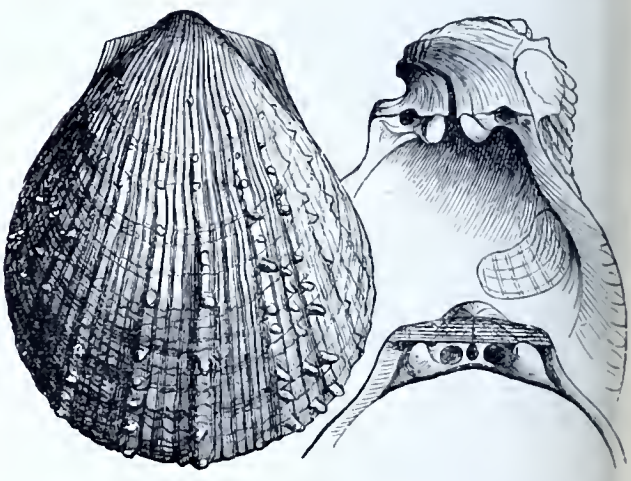


Fig. 669.

Spondylus tenuispina, Sandb. Oligocene; Waldböckelheim, near Kreuznach, Prussia. 1/1.

? *Pachypteria*, de Kon. Carboniferous. *P. nobilissima*, de Kon.

Family 35. **Dimyidae.** Dall.

Shell inequivalve, irregular, closed, auricles not differentiated, Ostreiform, dimyarian, sessile; shell substance sub-nacreous and fibrous; area amphidetic, obscure; ligament obsolete, resilium alivincular, internal; hinge armature Taxodont, obsolete; crural development feeble; gills filibranchiate, the inner direct filaments wanting, the outer not reflected; foot and byssus absent; anterior adductor distinct, small; posterior duplex, larger. Trias to Recent.

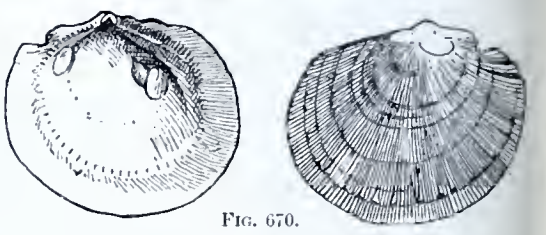


Fig. 670.

Dimya Deshayesiana, Rouault. Eocene; Pyrenees. Inner and outer views of right valve, 3/2 (after Rouault).

Dimya, Rouault (*Dimyodon*, Mun. Chalm.), (Fig. 670). The recent form inhabits deep water.

Family 36. **Limidae.** d'Orbigny.

Shell equivalve, auriculate, gaping, Pectiniform, monomyarian; shell substance fibrous, with minute tubules, not nacreous or prismatic; hinge edentulous, or with traces of Taxodont armature; area amphidetic, equal in both valves; ligament alivincular, resilium sub-internal; gills filibranchiate, with direct and reflected limbs; foot small

digitiform, usually byssiferous, the byssus passing through the gape of the valves. Carboniferous to Recent.

Lima, Brug. Shell inflated, with radial sculpture; beaks pointed, and separated by a lozenge-shaped area; edentulous. Carboniferous to Recent; maximum in Mesozoic (over 300 species).

Sub-genera: *Lima* s. s. (*Radula*, auct. non Gray), (Fig. 671). Shell with strong radial ribs.

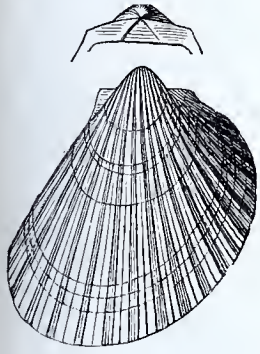


Fig. 671.

Lima pectinoides, Sow. Lower Lias; Balingen, Wurtemberg. 1/1.

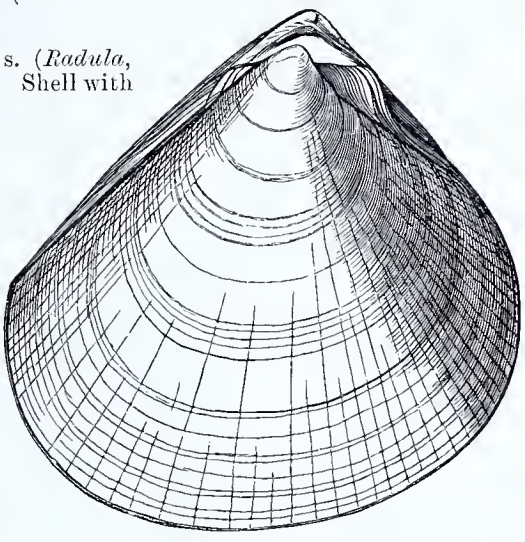


Fig. 672.

Lima (*Plagiostoma*) *gigantea*, Sow. Lower Lias; Göppingen, Wurtemberg. 2/3.

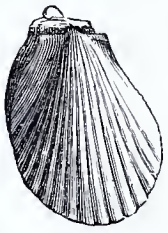


Fig. 673.

Lima (*Limatula*) *gibbosa*, Sow. Lower Oolite; Bayeux, Calvados.

Fig. 674.

Limaea duplicata, Goldf. Great Oolite; Langrune, Normandy.

Plagiostoma, Sow. (Fig. 672). Smooth or finely striated.
Limatula, Wood (Fig. 673). Medially ribbed, laterally smooth, valves not gaping.

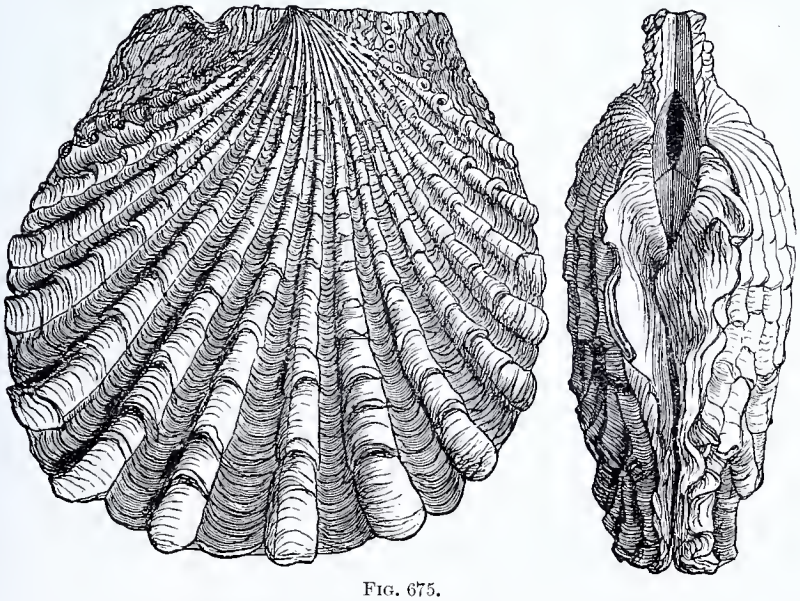


Fig. 675.

Ctenostreon proboscidea, Sow. Oxfordian; Dives, Calvados.

Limaea, Bronn (Fig. 674). Small, with Taxodont armature at the angles of the hinge. Lias and Recent.

Ctenostreon, Eichw. (Fig. 675). Compressed, irregular, thick-shelled, with coarse radial ribs. Upper Jura.

Superfamily 8. ANOMIACEA. Herrmannsen.

Shell monomyarian, not alate; edentulous or Isodont, usually sessile; shell substance nacreous, tubuliferous, with traces of a prismatic layer; area obscure, usually small, amphidetic; ligament obscure, with an alivincular internal resilium; gills filibranchiate, mantle lobes free; foot small, grooved, digitiform; dioecious; marine.

Family 37. Anomiidae. Gray.

Shell variable, irregular and inequivalve when sessile, byssiferous when young; in most genera the byssus becomes modified to a calcified or horny plug passing through a foramen in the attached valve, and fastened to other objects, a condition which may be permanent or transient; area small, amphidetic; ligament amphidetic, more or less internal, supplemented by an internal resilium, for which the crura serve as chondrophores, ali- or multivincular; hinge usually edentulous, rarely rugose, with amorphous interlocking rugosities; posterior adductor small, sub-central, in the sessile forms reinforced by the pedo-byssal muscles, which are modified for service as adductors. ? Devonian. Jura to Recent.

Anomia, Müll. Shell thin, sessile by the calcified byssus passing through a sinus or perforation in the right valve, conforming to the subjacent surface; the left valve more convex, with four muscular scars on a central area; a chondrophore in the lower valve. Jura to Recent.

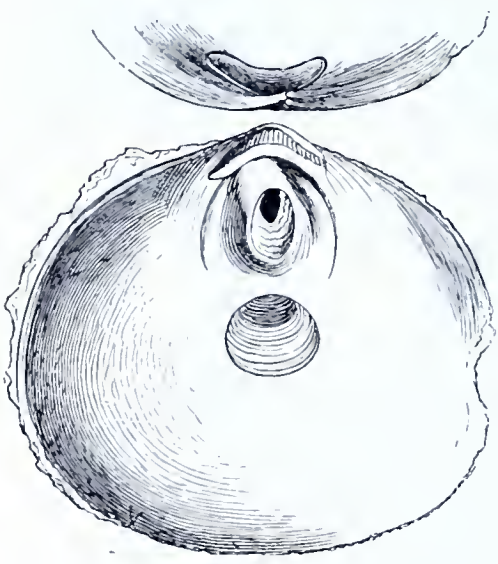


Fig. 676.

Carolia placunoides, Cantr. Eocene; Wadi el Tih, near Cairo, Egypt. Interior of both valves, 2/3.

? *Limanomia*, Bouch. Devonian. *Hypotrema*, d'Orb. Jura and Cretaceous. *Placunanomia*, Brod. Miocene to Recent.

Carolia, Cant. (Fig. 676). Shell orbicular, compressed, radially striated; right valve with a byssal foramen nearly closed in the adult; resilium much as in *Anomia*: adductor scar single. Eocene; Egypt.

Sub-genus: *Wakullina*, Dall. Smooth; byssal foramen obsolete; the resilium received on diverging crura in the upper valve. Oligocene; Florida.

Placenta, Retzius (*Placuna*, Brug.; *Placunema*, Stol.; *Pseudoplacuna*, Mayer). Shell free, orbicular, thin, very compressed; the resilium with long, unequal crura. Tertiary and Recent.

Ephippium, Bolten. Like *Placenta*, but the shell radially waved; young with a small byssal perforation, which becomes closed and obsolete in the adult. Tertiary and Recent.

Placunopsis, Morr. and Lyc. Shell rounded, imperforate, free, or sessile. Jura.

Hemiplicatula, Desh. (*Semiplicatula*, Fisch.); *Saintia*, Raine. Eocene. *Paranomia*, Conrad. Ripley Group. *Monia*, Gray. Miocene; California.

V. Dysodonta. Neumayr (emend.)

Superfamily 9. MYTILACEA. Ferussac.

Shell anisomyarian, usually equivalve, not alate or notched for a byssus, edentulous or Dysodont; shell substance sub-nacreous, rarely more or less prismatic, with a conspicu-

ous epidermis; area amphidetic or obscure; ligament parivincular, usually opisthodetic and external; gills usually filibranchiate; mantle lobes without ocelli, more or less free, generally with the anal siphon complete and the branchial incomplete; foot small, digitiform, grooved, byssiferous; monoecious; mostly marine.

Family 38. **Modiolopsidae.** Fischer (emend.)

Shell Modioliform, usually equivalve, free, thin, with sub-equal adductor scars; ligament deep-seated; hinge edentulous or Dysodont; sometimes byssiferous. Silurian to Cretaceous.

The heavier forms show an obtuse ridge or two extending from the beaks toward the basal margin. The pedal scars are separate from and behind the anterior adductors. The forms included here appear to be the prototypes of the *Mytilidae*, from which they differ chiefly in those characters that are common to most of the ancient types, such as the sub-equality of the adductor scars and their more dorsal situation. The recent *Idas* is very similar.

FIG. 677.

Modiolopsis modiolaris, Conr. sp. Ordovician; Cincinnati, Ohio. 1/1.

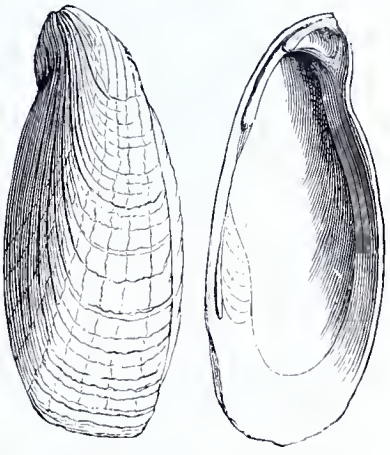


FIG. 678.

Myoconcha striatula, Goldf. Lower Oolite; Bayeux, Calvados. 1/1.

Modiolopsis, Hall (Fig. 677). Valves elongate-oval, closed, with nearly terminal beaks, narrow hinge plate, and edentulous hinge. ? Ordovician; Silurian.

Modiomorpha, Hall. Similar, but with a wider hinge plate, and single, oblique, elongate, posterior ridge-like tooth. Devonian.

Myoconcha, Sow. (Fig. 678). Hinge usually with an elongate cardinal, and a long, weak, lateral tooth in the right valve; otherwise resembling *Modiolopsis*. Carboniferous to Cretaceous.

? *Hippopodium*, Sow. Thick, inflated, ovate, concentrically waved. Hinge with a long, blunt, oblique, cardinal tooth, or edentulous; adductor scars strong. Jura.

Modiolodon, *Whiteavesia*, *Eurymya*, *Aristella*, and *Prolobella*, Ulrich; *Goniophora*, Phillips. Silurian and Devonian.

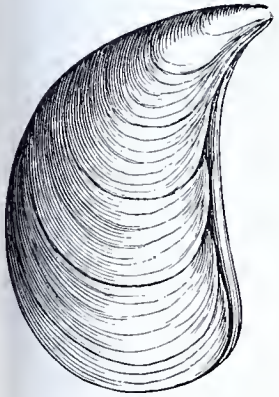


FIG. 679.

Mytilus subluevis, Sow. Great Oolite; Minchinhampton, England. 1/1.

Family 39. **Mytilidae.** Fleming.

Shell equivalve, very inequilateral, heteromyarian, slightly gaping, typically Dysodont; area amphidetic or none; ligament usually external, deep-seated; rarely with an alivincular internal resilium; pallial line simple; mantle lobes united below the anal siphon, otherwise free; generally byssiferous. Devonian to Recent.

Mytilus, Linn. (Fig. 679). Shell elongated, thin, with terminal pointed beaks; valves wider and rounded behind, gaping a little for the

byssus, smooth or radially sculptured, with smooth margins, conspicuous epidermis, and a thin nacreous layer; hinge with a few small teeth under the beaks, or edentulous. Trias to Recent.

Pachymytilus, Zitt. (Fig. 680). Shell thick, trigonal; the front margin deeply impressed. Upper Jura.

Modiola, Lam. (Figs. 681, 682). Like *Mytilus*, but the beaks not terminal, anteriorly rounded and wider. Devonian to Recent.

Fig. 680.

Pachymytilus pitosus, d'Orb. Coral-Rag; Coulange-sur-Yonne. 2/3.

Fig. 681.

Modiola aspera, Sow. Great Oolite; Langrune, Calvados. 1/1.

Fig. 682.

Modiola imbricata, Sow. Middle Jura; Balin, near Cracow, Austria. 1/1.

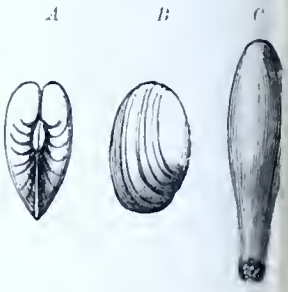


Fig. 683.

Lithophagus inclusus, Phill. sp. Great Oolite; Minchinhampton, England. *A*, *B*, Shell, 1/1. *C*, Cast of the burrow.

Sub-genera: *Modiolaria*, Lovén. Small, radially sculptured toward the ends, usually smooth toward the middle, Modioliform. Tertiary and Recent.

Crenella, Brown. Small, rounded, radially sculptured all over. Tertiary and Recent.

Stavelia, Gray. Recent. Valves spirally twisted.

Lithophagus, Meg. (*Lithodomus*, Cuv.), (Fig. 683). Sub-cylindrical, with rounded ends; perforating coral limestones and other substances, in which the animal forms flask-shaped excavations; casts of the latter are often found in the fossil state. Carboniferous to Recent.

Family 40. **Dreissensiidae**. Gray.

Shell Mytiliform, equivalve, of prevailingly prismatic substance; area linear, amphidetic; ligament sub-internal; anterior adductor and pedal protractors inserted on a myophoric septum; mantle lobes united to form anal and branchial siphons, and also ventrally with a pedal opening; pallial line usually simple; gills reticulate; otherwise as in Mytilus. Tertiary to Recent.

Dreissensia, Van Ben. (*Tichogonia*, Rossm.), (Fig. 684). Smooth, without a pearly layer, with a single apical septum; fluviatile and estuarine. Eocene to Recent; Europe.

Mytilopsis, Conr. Mytiliform, small, thin; Myophore for the pedal protractor distinct from that which supports the anterior adductor. Tertiary and Recent; America.

Fig. 684.

Dreissensia Brardi, Faujas. Miocene; Weissenau, near Mayence. 1/1.

Congeria, Partsch (Fig. 685). Sub-quadrate, heavy, large; myophores as in *Mytilopsis*. Very profuse in the Neocene of Eastern Europe.

Dreissensiomya, Fuchs. Notable for being the only example of the *Mytilacea* with a distinct pallial sinus. Miocene; Eastern Europe.

Septifer, Recluz. Valves with strong radial or divaricate sculpture. Marine. Tertiary and Recent.

The recent families, *Prasinidae* and *Modiolarcidae*, if their validity be confirmed,

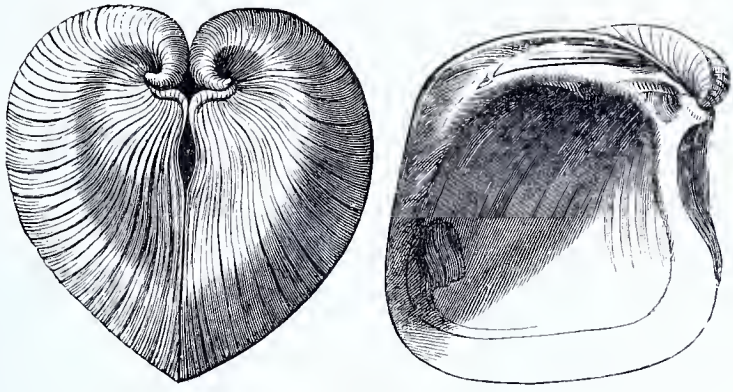


Fig. 685.

Congeria subglobosa, Partsch sp. Upper Miocene; Inzersdorf, near Vienna.

may find a place in this vicinity. *Prasina* and *Berthelinia* are reported from the Tertiary.

Order 2. ANOMALODESMACEA. Dall.

Superfamily 1. ANATINACEA. Dall.

Anomalodesmacea with V-shaped reticulate gills not secreting a calcareous tube exterior to the shell.

This group is divisible into sections as follows:—(*a*) *Eusiphonia*, with long siphons and the lithodesma, when present, at the anterior end of the internal resilium, and external to the mass of the resilium; and (*b*) *Adelosiphonia*, with short siphons, the lithodesma dividing the mass of the resilium mesially.

Section A. Eusiphonia.

Family 1. Pleuromyacidae. Zittel.

Shell slightly inequivalve, hinge with an obscure projection or edentulous, the cardinal border of one valve covering that of the other valve, which is supplemented by a sort of laminar nymph, the ligament sub-internal between them; area inconstant or obscure; pallial sinus present; valves closed or slightly gaping. Trias to Lower Cretaceous.

Pleuromya, Ag. (*Myacites*, auct.), (Figs. 686, 687). Posterior side longer, somewhat gaping, hinge margin with a thin horizontal lamina in each valve, the left inferior, the margin with a feeble notch behind the lamina; ligament parivincular. Trias to Lower Cretaceous; abundant, but seldom well preserved.

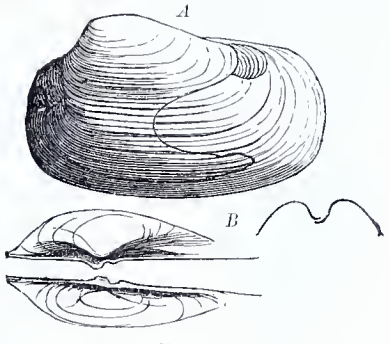


Fig. 686.

Pleuromya peregrina, d'Orb. Upper Jura; Chorostków, near Moscow. *A*, Internal cast, 1/1. *B*, Hinge.

Gresslya, Ag. (Fig. 688). Like *Pleuromya*, but the right hinge margin projecting over the left, anterior side short, wide; ligament parivincular, almost internal, attached to an internal nymph-like callosity in the right valve, which appears as a groove on internal casts. Abundant in the Jura, especially in the Lias.

Ceromya, Ag. (Fig. 689). Cordate, inflated, with rather anterior, prosogyrous beaks; hinge margin of the right valve superior, edentulous, but with a blunt

Fig. 687.

Pleuromya tenuistriata, Ag. Middle Jura, Zajaczki, Poland. 1/1.

Fig. 688.

Gresslya latirostris, Ag. Lower Oolite; Tannie, Sarthe. 1/1.

Fig. 689.

Ceromya, cf. *Aalensis*, Quenst. Middle Jura; Kneuttingen, Lorraine. Hinge, 1/2.

elongated process in front of an internal callosity. Chiefly occurring as casts. Jura.

Family 2. **Pholadellidae.** Miller (emend.)

Shells obovate, usually attenuated behind and slightly gaping, hinge margin thin, edentulous, ligament parivincular, external; posterior adductor scar large. Palaeozoic.

Allorisma, King. Elongate, arcuate, the pallial line sinuated, anterior side shorter, sometimes with a lunule; sculpture strongest mesially. Carboniferous and Permian.

Rhytimya, Ulrich. Elongate, sub-quadrate, concentrically waved, the waves stronger anteriorly; sculptured on the posterior half with radiating series of granules; lunule very narrow. Silurian.

Pholadella, Hall; *Cimitaria*, Hall. Devonian.

Family 3. **Pholadomyacidae.** Gray.

Shell substance nacreous and cellulo-crystalline; gills completely united behind, forming a septum below the anal

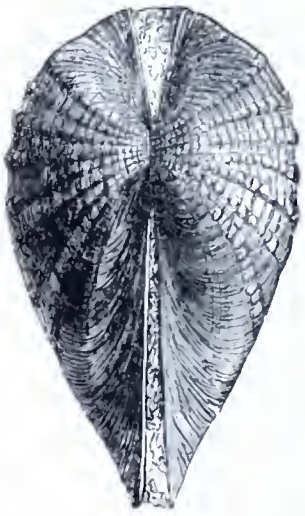


Fig. 690.

Pholadomya Murchisoni, Sow. Middle Jura; Piezchnow, Poland. 1/1.

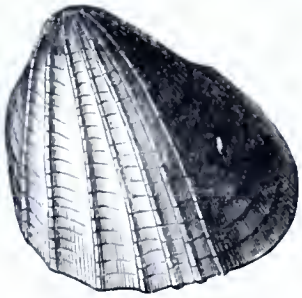


Fig. 691.

Pholadomya deltoidea, Ag. Middle Jura; England. 1/2.

Fig. 692.

Pholadomya Puschi, Goldf. Oligocene; Tölz, Bavaria. 2/3.

chamber; foot small, with an opisthopodium: siphons long, united to their tips, not wholly retractile, naked; ventral commissure of the mantle with a pedal and an opistho-

podial foramen. Shell thin, equivalve, gaping, edentulous, or with an obscure sub-umbonal tubercle; ligament, and resilium external, opisthodetic, seated on nymphae; area obsolete or obscure, not amphidetic; beaks entire; pallial sinus well marked; marine. Trias to Recent.

Pholadomya, Sow. (Figs. 690-692). Shell thin, sub-ovate, with radial and concentric sculpture, inflated, and with rather prominent beaks; hinge edentulous, or with an obscure thickening; scars feeble, pallial sinus moderately deep. In the posterior dorsal region the radial sculpture is usually feeble or absent. Lower Lias to Recent; formerly very abundant, but now represented by but a single species from the Antilles.

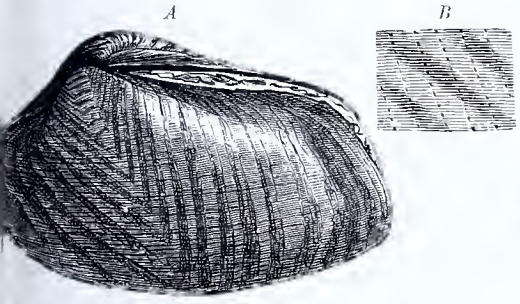


Fig. 693.

Goniomya Duboisi, Ag. Inferior Oolite; Bayeux, Calvados. *A*, Shell, 1/1. *B*, Surface showing punctations, magnified.

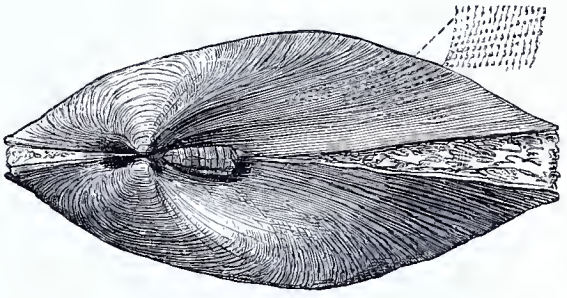


Fig. 694.

Homomya (*Areomya*) *calceiformis*, Ag. Inferior Oolite; Les Moutieux, near Bayeux, Calvados. 2/3.

Procardia, Meek. Includes those forms with an escutcheon. Jura.

Goniomya, Ag. (Fig. 693). With V-shaped sculpture. Lias to Cretaceous; very plentiful in Middle and Upper Jura.

Homomya, Ag. (*Areomya*, *Myopsis*, Ag. p.p.), (Fig. 694). Distinguished from the typical *Pholadomyas* by its smooth or very finely sculptured shell, without ribs. Trias to Cretaceous.

(?) *Machomya*, *Pleetomya*, Loriol; *Mactromya*, Ag. Jura and Cretaceous.

Family 4. **Anatinidae.** Dall.

Soft parts like Pholadomya, the foot small and grooved, ventral foramina small, and the siphons with a horny integument, not entirely retractile. Shell sub-equivalve, truncate, or gaping behind, edentulous, the resilium internal between two spoon-like chondrophores vertically directed and often supported by buttresses; ligament obsolete or absent; area obsolete; beaks transversely fissured; pallial sinus well marked; monoecious; marine. Jura to Recent.

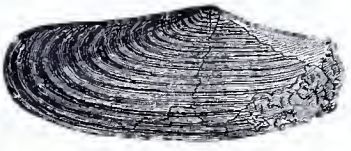


Fig. 695.

Anatina producta, Zittel. Upper Cretaceous; Gosau Valley, Austria.

Anatina, Lam. (*Platymya*, *Cereomya*, Ag.; *Plicomya*, Stol.), (Fig. 695). Shell thin, nearly equivalve, concentrically but feebly sculptured, posterior side shorter than the anterior. Jura to Recent.

Periplomya, *Anatimya*, Conrad; *Rhynchomya*, Agassiz. Cretaceous.

Family 5. **Periplomidae.** Dall.

Shell sub-naereous, conspicuously inequivalve, nearly closed, edentulous; the resilium internal, between two anteriorly or vertically directed chondrophores, often buttressed, the lithodesma rarely wanting; ligament and area absent; beaks fissured; pallial sinus

broad and shallow; siphons separated to their bases, naked and wholly retractile; monoecious; marine. Tertiary and Recent.

Periploma, Schum. Shell oval or rounded, smooth or with faint concentric striae; lithodesma present. Tertiary and Recent.

Cochlodesma, Couth. Buttress of the chondrophore posteriorly directed; no lithodesma. Pliocene and Recent.

Bontaca, Leach (*Ligula*, p.p. Mont.); *Tyleria*, Adams. Recent.

Family 6. **Thraciidae.** Dall.

Shell earthy and cellulo-crystalline, not nacreous; inequivalve, thin, edentulous, often with a granular surface; ligament and resilium chiefly external, opisthodetic, parivincular, seated on posteriorly directed nymphae; area absent, beaks usually entire; valves nearly closed, with pallial sinus; mantle openings small; siphons long, separated to their tips, naked; monoecious; marine. Jura to Recent.

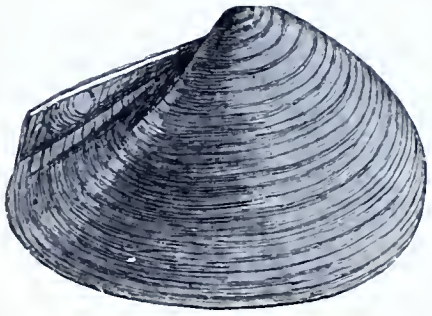


Fig. 696.

Thracia incerta, Ag. Upper Jura; Pruntrut, Switzerland. 1/1.

Thracia, Leach (*Corimya*, Ag.), (Fig. 696). Shell smooth or concentrically striated, with granular surface, usually more or less rostrate. Trias to Recent.

Cyathodonta, Conr. Shell with oblique or angular waves of sculpture, otherwise like the preceding. Tertiary and Recent.

Bushia, Dall; *Asthenothaerus*, Carpenter. Recent.

Family 7. **Myochamidae.** Dall.

Shell very inequivalve, free or sessile, solid, sub-nacreous, edentulous, the dorsal margins of one valve overlapping those of the other, which fit into corresponding depressions in the shell wall; ligament amphidetic, external or absent; resilium internal, alivincular; area amphidetic or obsolete, a false area formed on each side of the beaks by the flattened cardinal margin of the valves; shell closed; pallial sinus small. Tertiary and Recent.

The gills and siphons of *Myochama*, Stutchbury, which lives sessile on shells, are more like those of *Thracia* than of the *Pandoridae*, with which it has usually been associated. The anatomy of *Myodora* is unknown. Its minute area curiously recalls that of *Spondylus*, and it is free.

Section B. Adelosiphonia.

Family 8. **Pandoridae.** Gray.

Shell compressed, inequivalve, free, solid, with nacreous and prismatic layers; the dorsal edges of the valves overlapping, but not socketed, with dentiform crural ridges on either side of the resilium, but no true teeth; ligament amphidetic, external, obsolete; resilium internal, opisthodetic, usually reinforced on its anterior surface by a mesial elongate lithodesma; area none; valves closed, beaks entire, pallial line simple; marine. Cretaceous to Recent.

Pandora, Brug. Diverging crura without connecting lamellae; buttress and lithodesma absent. The sub-genus *Kennerlia* has a lithodesma. Tertiary and Recent.

Coelodon, Carp. Crura of the left valve united by a transverse lamella. *Clidiophora*, Carp., has the hinge plate buttressed and a lithodesma. Tertiary and Recent.

Family 9. **Lyonsiidae.** Dall.

Shell inequivalve, thin, sub-nacreous, edentulous; ligament obsolete, the resilium internal, uniting the edges of a long, mesial lithodesma to a narrow chondrophoric submarginal ridge on each valve; beaks entire, valves nearly closed, pallial sinus distinct; marine. Tertiary and Recent.

Lyonsia, Turton. Small, thin, posteriorly elongate with delicate radiating sculpture. Tertiary and Recent.

Entodesma, Phillippi. Recent. *Actinomya*, Mayer. Eocene; North America.

Family 10. **Lyonsiellidae.** Dall.

Shell nearly equivalve, sub-nacreous, with a more or less distinct tubercle in front of the resilium on the dorsal margin; ligament obsolete, cartilage internal with a large lithodesma; area obscure or absent; beaks entire; valves almost closed; pallial sinus obsolete. Tertiary and Recent.

Halicardia, Dall; *Lyonsiella*, Sars. Chiefly Recent.

Superfamily 2. **ENSIPHONACEA. Dall.**

Differing from Anatinacea by the formation of a calcareous tube, which may include one or both of the valves, and is usually furnished with a perforated anterior disk surrounded by a more or less complete fringe of small calcareous tubules.

Family 11. **Clavagellidae.** D'Orbigny (emend.)

Shell degenerate, extremely specialised for a burrowing life; valves nacreous, free when young; when adult, one or both merged in a calcareous tube anteriorly discoid and fringed, with a narrow pedal foramen in the middle of the disk; free valves edentulous, the ligament external, opisthodetic, supported by nymphs; pallial line sinuate; tube frequently encrusted with extraneous material; marine. Cretaceous to Recent.

Clavagella, Lam. (*Bryopa*, Gray; *Stirpulina*, Hol.), (Fig. 697). One of the valves not attached to the tube and adductor muscles persistent. Cretaceous to Recent.

Brechites, Guett. (*Aspergillum*, Lam.) Both valves merged in the tube, anterior adductor reduced, and the posterior obsolete. Pliocene and Recent.

Fig. 697. *Clavagella Caillati*, Desh. Eocene; Grignon. 1/2 (after Deshayes).

Superfamily 3. **POROMYACEA. Dall.**

Anomalodesmacea having modified foliobranch or lamellar gills, slightly or not at all reticulated, and frequently degenerate or even absent; valves free, without a calcareous tube external to them; mantle lobes united, with siphons and a pedal, but no opisthopodial foramen; the cartilage reinforced below by a lithodesma.

Family 12. **Euciroidae.** Dall.

Shell sub-equivalve, nacreous, and cellulo-crystalline, externally granulose; hinge with a strong tubercle in the right valve before the resilium, and the dorsal margins modified to overlie and underlie each other; ligament obsolete; resilium opisthodetic,

internal, with a strong lithodesma ventrally: area obscure or absent; a depressed false lunule before the beaks; valves closed, pallial sinus shallow, obscure; siphons short, separate: marine. Tertiary to Recent.

Pecchiolia, Menegh. Shell heavy; beaks spirogyrate, distant; sculpture radial. Eocene; Alabama. Miocene; Europe.

Eucirsa, Dall. Recent, abyssal.

The genera *Verticordia*, Wood.; *Trigonulina*, d'Orb.; *Haliris*, Dall; and ?*Allopagus*, Stol. (*Hippagus*, Desh. non Lea), are included under the family *Verticordiidae*. Tertiary and Recent.

Family 14. **Poromyacidae.** Dall.

Shell rounded, nacreous, and cellulo-crystalline, granular, or smooth externally; hinge with obscure tubercles in front of the resilium; ligament external, opisthodetic; resilium sub-internal below the ligament, with a small lithodesma; area obscure or absent; a depressed false lunule in front of the beaks; valves nearly or entirely closed; pallial sinus small or obsolete; marine. Cretaceous to Recent.

Liopistha, Meek (*Cymella*, *Psilomya*, Meek), (Fig. 698). Equivalve, oval, thin, inflated, concentrically or radially striated, gaping and compressed behind; beaks prominent, incurved; hinge with a nymph and projecting process on each side; ligament sunken, partly external. Cretaceous.

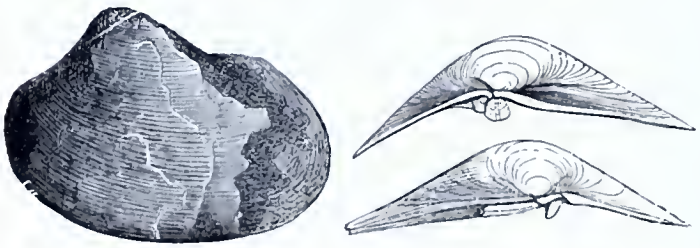


Fig. 698.

Liopistha frequens, Zitt. Upper Cretaceous; Gosau, Austria. 1/1.

?*Basterotia*, Mayer (*Eucharis*, Recluz non Péron). Valves sub-equal, closed, with a strong tooth in the right and two in the left; surface granular; form trapezoid. Miocene and Recent.

Poromya, Forbes (*Embla*, Lovén). Ovate, plump, surface granular; pallial line irregularly widened, not sinuate. Eocene and Recent.

Dermatomya, Dall. Surface smooth, with a conspicuous periostracum; pallial line sinuate. Recent, abyssal.

Cetomya, *Cetoconcha*, Dall (*Silenia*, Smith). Recent, abyssal.

Family 15. **Cuspidariidae.** Dall.

Shell sub-equivalve, rostrate, earthy, or cellulo-crystalline, rarely with surface granulations; hinge edentulous or with sub-umbonal tuberculation, sometimes buttressed; ligament sub-internal, anterior to the beaks or obsolete; resilium internal, with a mesial or ventral lithodesma; area amphidetic or obscure; valves closed except at the tip of the rostrum; pallial line simple; siphons united; marine. Jura to Recent.

Fig. 699.

Cuspidaria cuspidata, Olivi. Miocene; Baden, near Vienna. 1/1.

Cuspidaria, Nardo (*Neaera*, Gray), (Fig. 699). Shell concentrically sculptured; hinge with a small posteriorly inclined chondrophore in each valve, and an elongated ridge behind it; ligament always anterior to the beaks when present. Jura to Recent.

Sub-genera: *Cardiomya*, Adams; with radial sculpture and a posterior lateral tooth in the right valve. *Leiomya*, Adams; smooth, with an anterior cardinal in each valve, and

anterior and posterior laterals in the right valve only. *Plectodon*, Carp. ; surfaee granulated. *Rhinoclama*, D. and S. ; like *Plectodon*, but without eardinal teeth. *Tropidomya*, D. and S. ; hinge with a bnttress, one anterior cardinal, but no lateral in either valve. *Halonympha*, D. and S. ; right valve with a single eardinal, no other teeth in either valve, a eonspieuous posterior laminar buttress in eaeh valve. *Luzonia*, Dall. Tertiary and Reeent.

Myonera, Dall and Smith. Shell thin with concentric waves and sparse radial ribs ; hinge edentulous ; rostrum short, rounded. Recent, abyssal.

? *Corburella*, Lycett. Middle Jura. *Spheniopsis*, Sandberger. Tertiary.

Order 3. TELEODESMACEA. Dall.

A. Pantodonta.

Laterals exceeding two in any one group.

Family 1. **Allodesmidae.** Dall. (*Cycloconchidae*, Ulrich).

Shell rounded ; valves equal, free, closed, with feeble coneentric sculpture ; area linear, amphidetic ; ligament sub-external, parivincular, opisthodetic ; adductor scars sub-equal, pedal scars above and distinct from the adductors ; pallial line entire ; hinge with one or two lateral laminae on each side of the beak, the posterior below the ligament, reeeived into eorresponding grooves on the right valve ; cardinal teeth radially grooved ; one or two in each valve, those in the right valve stronger. Silurian.

This family, as suggested by Neumayr, probably exemplifies the first step in the development of the Teleodesmacean hinge. But it must be admitted that its amphidetic though linear area, the oeeasional multiplieation to three of the lateral laminae, and the sub-ligamentary location of the hinder laminae, are very reminiseent of the prevalent Silurian Selizodont type, and the family ean be admitted to the *Teleodesmacea* only as a probable aneestor, rather than a perfeetly developed type of the modern assemblage.

Orthodontiseus, Meek (*Cyeloconcha*, Miller ; ? *Anodontopsis*, M'Coy). Silurian ; Ohio.

Allodesma, Ulrich. Like *Orthodontiscus*, but more elongate, the beaks more anterior, the anterior adductor scar buttressed by a radial ridge, and the anterior lateral teeth short or absent. Ordovician.

B. Diogenodonta.

Laterals normally one or two, and cardinals three or less, in any one group.

Superfamily 1. CYPRICARDIACEA. Dall.

Lobes of the mantle partly closed ventrally ; anterior lateral laminae absent, or grouped with the cardinal teeth, short and obscure.

Family 2. **Pleurophoridae.** Dall.[1]

Shell substance cellulo-erystalline ; valves equal, free, elosed ; adductor scars sub-equal, free from the pedal sears ; pallial line entire, or feebly sinuated ; area obscure ; ligament external or seated in a groove, parivineular ; margins of the valves usually plain ; hinge with one left and two right posterior laminae, the anterior laminae absent or confused with the cardinals ; two or three cardinal teeth in each valve, of which the posterior in both valves is sub-parallel to the dorsal shell margin, and in the right valve is usually bifid. Mantle with a moderate pedal and two siphonal openings, the latter usually not produced into tubes. Devonian to Recent.

[1] *Cyprinidae*, p.p. of authors, but this name eannot be used.

This family, so well known under the preoccupied name *Cyprinidae*, probably shared the same origin as the *Astartidae*, and the two do not definitely separate until the Jura. The position of the Palaeozoic ancestors is necessarily doubtful, and they are placed differently by different authors. The group may be conveniently divided into two sub-families: *Pleurophorinae* and *Veniellinae*.

Pleurophorus, King (Fig. 700). Elongated, sub-rectangular; beaks sub-terminal; surface smooth or with radial sculpture; hinge with two cardinal teeth in each valve;

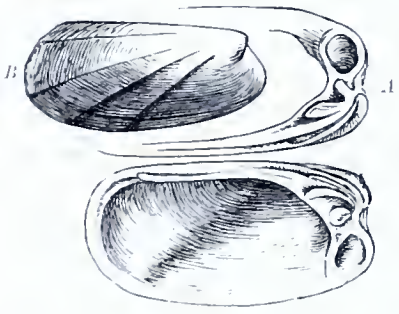


Fig. 700.

Pleurophorus costatus, King. Permian; Byers Quarry, England. *A*, Shell, 1/1 (after King). *B*, Internal cast from Gera, Thuringia (after Geinitz).

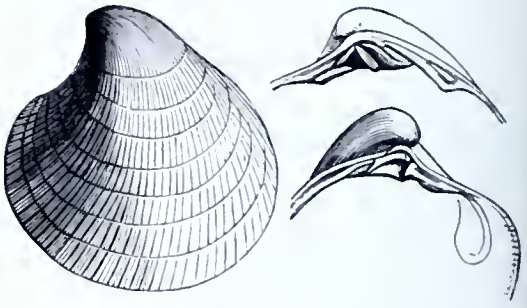


Fig. 701.

Anisocardia elegans, Mun.-Chalm. Kimmeridgian; Cap de la Hève, near Havre. 1/1.

anterior adductor scars deep, with a buttress-like ridge behind it. Devonian to Trias; especially abundant in the Permian.

Cypricardella, Hall (*Microdon*, Hall); *Mecynodon*, Keferst.; *Cypricardinia*, Hall. Devonian. *Astartella*, Hall. Carboniferous.

Anisocardia, Mun.-Chalm. (Fig. 701). Rounded or trapezoid, plump, smooth or radially striate; posterior slope sometimes keeled; hinge with a strong sometimes bifid right cardinal behind, and an anteriorly directed front cardinal; left

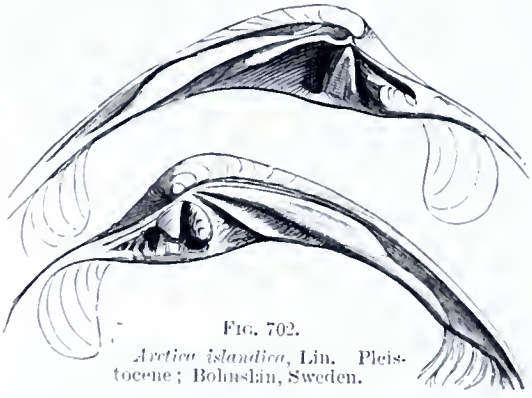


Fig. 702.

Arctica islandica, Lin. Pleistocene; Bohuslän, Sweden.

Fig. 703.

Venilicardia cordiformis, d'Orb. Gault; Seignelay, Yonne.

Fig. 704.

Veniella tumida, Nyst. Crag; Antwerp

valve with a forwardly directed anterior and a posterior cardinal tooth. Jura to Tertiary.

Roudairia, Mun.-Chalm. Like *Trapezium*, but with a sharp keel and smooth area behind, anteriorly with concentric ridges; right posterior cardinal bifid. Upper Cretaceous.

Trapezium (Humph.), Megerle (*Libitina*, Schum.; *Cypricardia*, Lam.) Shell elongate, trapezoidal, concentrically, or more rarely radially sculptured, often with a posterior keel; three cardinal teeth in each valve, the posterior in the right valve often bifid. Jura to Recent.

Plesiocyprina, Mun.-Chalm. Jura. *Cicatrea*, Stol. Cretaceous. *Coralliophaga*, Blainv. Tertiary and Recent.

Arctica, Schum. (*Cyprina*, Lam.), (Fig. 702). Oval or rounded, inflated, concentrically striated; beaks prominent, curved, cardinals three in each valve, the left posterior often bifid, the middle left cardinal largest, and the posterior ridge-like. Abundant in the Jura and Cretaceous, and represented by one or two living species.

Venilicardia, Stol. (Fig. 703). Cretaceous. *Pygocardia*, Mun.-Chalm. Tertiary.

Veniella, Stol. (*Venilia*, Morton; (?) *Goniosoma*, Conr.), (Fig. 704). Left valve with the anterior cardinal strong, sub-triangular. Cretaceous and Tertiary.

Superfamily 2. ASTARTACEA. Dall.

Lobes of the mantle free ventrally; lateral laminae obscure, when present distant from the cardinals.

Family 3. Curtonotidae. Dall.

Shell short and heavy, with sub-terminal beaks; valves free, equal, closed; area obscure; ligament as in the Astartidae; adductor scars, especially the anterior, deep; pallial line simple; hinge plate broad, without lateral laminae; the formula of the cardinals $\frac{\text{L}0101}{\text{R}1010}$ or $\frac{\text{L}010}{\text{R}101}$. Devonian and Carboniferous.

This group is inserted conformably with the opinion of Neumayr, who regards it as the radical of the *Astartidae*.

Curtonotus, Salter. Oval, cardinal border thick, with one very strong tooth in the left, and a strong anterior and thin posterior tooth in the right valve. Scars of the adductors strong, especially the anterior. Devonian; England.

Prosocoelus, Keferst. Devonian. *Protoschizodus*, de Kon. Carboniferous.

Family 4. Astartidae. D'Orbigny (emend.)

Shell substance cellulo-crystalline, with a pronounced epidermis; shell rounded or sub-triangular, usually with concentric or not radial sculpture; valves equal or sub-equal, free, closed; area distinct; ligament and resilium external, parivincular, opisthodetic; beaks prosocoelous; adductor scars sub-equal, with a distinct anterior pedal scar; pallial line simple; hinge plate distinct, hinge with anterior and posterior lateral teeth and their respective sockets, usually more or less obsolete; cardinal teeth not bifid at the summit, the terminal teeth frequently obsolete. Lobes of the mantle free ventrally, not produced into siphons. Trias to Recent.

Fig. 705.

Astarte Voltzi, Ziet. Middle Jura; Gundershofen, Alsace. 1/1.

Astarte, Sow. (*Crassina*, Lam.), (Fig. 705). Roundly triangular or oval, rather compressed, thick; smooth or concentrically sculptured; lunule impressed; right anterior cardinal strong.

A number of genera have been associated with *Astarte* which probably belong elsewhere. The following sub-genera, however, are worthy of recognition:—*Coelastarte*, Böhm; *Preconia*, Stol.; *Crassinella*, Bayle non Guppy (Fig. 706); *Prorokia*, Böhm. Jura. *Eriphyla*, Gabb. Cretaceous. *Grotriania*, Speyer; *Goodallia*, Turton (Fig. 708); *Rhectocyma*, Dall; *Woodia*, Deshayes (Fig. 707). Tertiary and Recent.

Opis, Defr. (Fig. 709). Trigonal, cordate, smooth, or concentrically striate; beaks prominent, prosocoelous; lunule very deep, bordered by a keel; cardinal teeth long, narrow (2 : 1). Trias to Cretaceous.

Opisoma, Stol. Jura. *Seebachia*, Neumayr. Cretaceous.

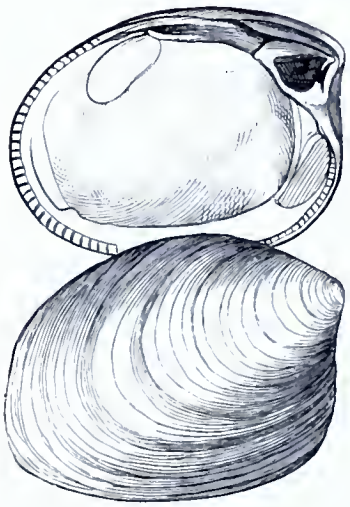


Fig. 706.

Astarte (*Crassinella*) *obliqua*, Desh. Inferior Oolite; Bayeux, Calvados.

Fig. 707.

Woodia profunda, Desh. Eocene; Aizy, near Laon. *A*, Hinge, enlarged. *B*, Shell.

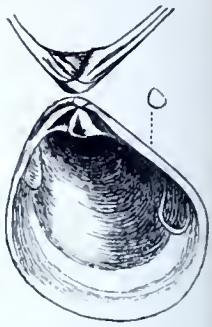


Fig. 708.

Astarte (*Goodallia*) *miliaris*, Defr. Eocene; Grignon, near Paris (after Deshayes).

Fig. 709.

Opis Goldfussiana, d'Orb. Upper Jura; Nattheim.

Family 5. **Crassatellitidae**. Dall.

Shell as in the Astartidae, but the valves always somewhat unequal, and usually more or less rostrate, the beaks compressed, erect, or opisthocoelous; ligament internal, more or less obsolete, resilium large, wholly internal, attached at each end to a chondrophoric pit in the hinge plate behind the cardinal teeth; lateral teeth and sockets usually alternated in the valves, the hinge plate heavy, flat; the posterior cardinal in the right valve very small or obsolete, with no distinct socket in the opposite valve; full cardinal formula $\frac{\text{L } 1010}{\text{R } 10\overline{10}1}$. Lower Cretaceous to Recent.

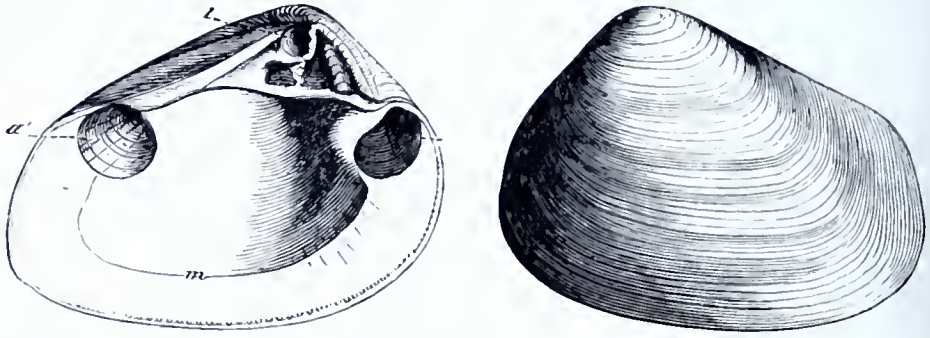


Fig. 710.

Crassatellites plumbea, Chem. sp. Eocene (Calcaire Grossier); Damery, near Epernay. 2/3.

The earlier forms of this family have a small resilium close to the nearly marginal ligament. With time, later ones show a gradual descent of these organs, until in some of the

more specialised modern representatives there is no appreciable ligament remaining, and the resilium has become large and deeply immersed. The parallelism between this group and the *Mactridae*, in the gradual immersion of the ligament, could hardly be more complete.

Crassatellites, Kruger (*Crassatella*, Lam., 1819, non Lam., 1799), (Figs. 710, 711). Cretaceous to Recent; represented by about seventy fossil and forty living species.

Triodonta, Koenen. Oligocene. *Scambula*, Conrad; *Remondia*, Gabb (*Stearnsia*, White); *Anthonyia*, Gabb; *Crassatellina*, Meek. Cretaceous.

? *Ptychomya*, Ag. Like *Crassatellites*, but with radial sculpture and three cardinals in each valve. Cretaceous.

Crassinella, Guppy non Bayle (*Gouldia*, auct. non Adams; *Pseuderiphyla*, Fisch.) Small, sub-triangular, very compressed, concentrically ribbed. Tertiary and Recent.

FIG. 711.

Crassatellites Bronni, Merian. Oligocene; Weinheim, near Alzey. 1/1.

Superfamily 3. CYRENACEA. Tryon.

Cypricardians which have become specialised for fresh or brackish water conditions, and, as usual in such cases, have developed great variability of character.

Family 6. Cyrenidae. Gray.

Shell porcellanous, with a conspicuous epidermis, usually with concentric sculpture; valves equal, free, closed, usually with plain margins; area obscure or none; ligament and resilium external, parivincular, opisthodetic; adductor scars sub-equal, separate from the pedal; pallial line simple or with a small sinus; hinge with anterior and posterior laterals usually double in the right, single in the left valve, distinctly separated from the cardinals; cardinal teeth bifid at the summit, three in each valve when none are obsolete. Mantle open ventrally, the siphons distinctly developed, short, more or less united. Lias to Recent.

Many of these forms merge with one another as we recede in time. The recent American forms and many fossils show a pallial sinus; oriental species are generally without it. In some fossils the laterals of the right valve are not double.

Cyrena, Lam. Rounded, sub-equilateral, plump, concentrically sculptured, with smooth margins; cardinals three, the laterals smooth. Lias to Recent (300 species); maximum in the Cretaceous and onwards.

FIG. 712.

Corbicula fluminalis, Müll. sp. Pleistocene; Teutschenthal, near Halle, Saxony.

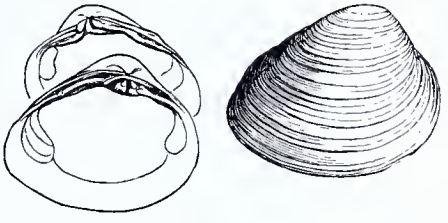


FIG. 713.

Corbicula semistriata, Desh. Oligocene (Cyrena marls); Flonheim, near Alzey. 1/1.

Sub-genera: *Corbicula*, Megerle (Figs. 712, 713). Smaller than *Cyrena*, and the laterals sharply cross-striated. *Egeta*, Adams. Compressed, elongated, thin; almost rostrate. Recent; marine.

Batissa, Gray. Like *Cyrena*, but the right anterior and left posterior cardinals feeble or obsolete; anterior laterals very short, posterior ones elongated. Upper Cretaceous of Oregon, and living in Indo-Pacific region.

Veloritina, *Leptesthes*, Meek. Laramie Group. *Velorita*, Gray. Recent. The relations of the recent *Galatea*, Brug., and *Fischeria*, Bernardi, do not seem to be positively fixed.

Family 7. **Sphaeriidae.** Dall.

Shell as in the Cyrenidae, but small, with a feeble, short ligament, a simple pallial line, and no hinge plate; cardinal teeth usually two in each valve, variable, very thin, often nearly parallel to the hinge margin or defective in part of the series; laterals as in the Cyrenidae, distinct. Upper Cretaceous to Recent.

Sphaerium, Scop. (*Cyclas*, Brug.) Branchial siphon complete; shell inflated, rounded. Upper Cretaceous to Recent.

Sub-genus *Eupera*, Bgt. Shell compressed, trapezoid. Tertiary and Recent; sub-tropical.

Pisidium, Pfr. Shell inequilateral; branchial siphon merged with the pedal opening. Eocene to Recent.

Superfamily 4. CARDITACEA. Menke.

This group appears to have branched off from the Astartoid radical in the early Mesozoic, forming in one sense a sort of parallel series with the Astartidae, with which it is contrasted most obviously by its prevailingly radial sculpture and prolonged posterior cardinal tooth.

Family 8. **Carditidae.** Gill.

Shell as in the Astartidae, but usually with radial sculpture, the pedal adjacent to the anterior adductor scar; ligament external, parivincular; resilium usually included in the ligament, rarely internal; hinge fully developed, with the laminae as in the Astartidae, and usually obsolete; the anterior cardinal often obsolete, the posterior prolonged parallel with the dorsal margin even below the ligament. Full cardinal formula $\frac{\text{L}01010}{\text{R}10101}$. Marine. Trias to Recent.

The earlier forms approach the *Astartidae* and *Pleurophoridae* so closely that they can hardly be discriminated.

Cardita, Brug. Elongate, quadrate, with prominent, very anterior beaks; sculpture radial and usually imbricated, commonly with a lunule; inner margins dentate; cardinals long and oblique. Trias to Recent.

Fig. 714.

Palaeocardita crenata, Munst. sp. Upper Trias; St. Cassian, Tyrol.

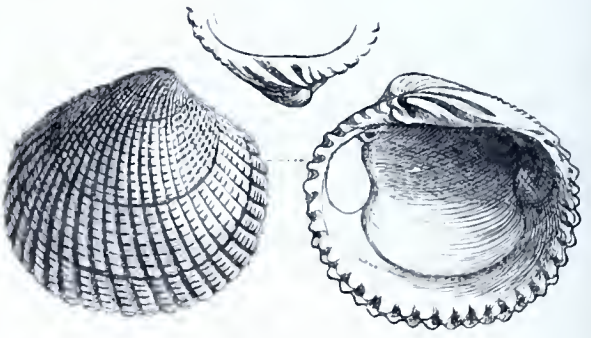


Fig. 715.

Venericardia imbricata, Lam. Eocene; Grignon, near Paris.

Palaeocardita, Conr. (Fig. 714). Like *Cardita*, but with a posterior lateral tooth. Trias and Cretaceous.

Venericardia, Lam. (Fig. 715). Rounded or cordate; lateral teeth absent or obsolete. Cretaceous to Recent.

Carditamera, Conr. Elongated, sub-mytiliform. *Pleuromeris*, Conr. Small, equilateral, trigonal. *Calyptogena*, Dall. Ovoid, smooth externally. *Carditella*, Smith. Small, with internal ligament. All Tertiary and Recent. *Thecalia*, Adams; *Milneria*, Dall. Females with a shelly marsupium. Recent.

Superfamily 5. CHAMACEA. Geinitz.

Carditian forms specialised for a sessile habit, usually with exceptionally spiral growth, and very unequal valves. Marine.

Family 9. Chamidae. Lamarck.

Shell substanee three-fold, the inner layers porcellanous and tubular, the middle obscurely prismatic, the external eellulo-crystalline with reticulated tubules and an inconspieuous epidermis; valves unequal, irregular, one of them sessile; elosed, usually rounded in form with eonspieuous seulpture, often differing in the opposite valves; adductor scars sub-equal, elongate, pedal sears minute, distant; ligament and resilium external in a deep groove, parivincular, opisthodetie; area distinct, prosodetie; beaks more or less spiral, prosogyrous; pallial line simple; hinge plate heavy, areuate; hinge frequently with a minute or obsolete posterior lamina, ehiefly in the fixed valve; eardinals one or two in the free valve, two with an intermediate soeket in the fixed valve; the anterior eardinal broad, usually deeply grooved or multifid, the posterior simple, long and curved parallel with the dorsal border; siphonal orifices not produeed into tubes; adductors each composed of two elements. Cretaceous to Recent.

Either of the valves of *Chama* may be the sessile one, but the teeth in the fixed valve, whether right or left, are always the same, and similarly with the free valve. The fixation is generally by the left valve.

Chama, Lin. (Fig. 716). Nepionic shell rounded. Ligament sometimes continued to the point of the beaks, as in other bivalves with gyrate umbones; form rounded, attached valve deeper and larger, the free valve flatter; margins usually cross-striated, surface lamellar or spinose; adductor scars large, not elevated. Cretaceous to Recent; maximum in Eocene.

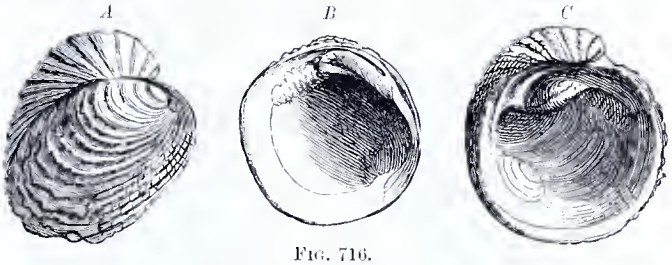


Fig. 716.

Chama squamosa, Lam. Eocene; Hampshire. 1/1.

Eehinoehama, Fisch. Nepionic shell elongated, having the form, hinge, and other characters of *Cardita*; attached when adolescent, free in the young and adult stages. Valves sub-equal and similar; surface vermiculate, spinose, with radial ribs. Oligocene and Recent.

Family 10. Diceratidae. Dall.[1]

Resembling Chama, but with the adductors usually borne on myophoric laminae, or projections which are prolonged into the umbonal eavity below the hinge plate; valves

[1] For the *Chamacea* and *Rudistae*, Neumayr proposed the term *Pachydonta*. For special literature see: *Zittel, K. A. von*, Die Bivalven der Gosaugebilde (Denkschr. Akad. Wissensch. Wien, Bd. XXIV.), 1864.—*Gemmellaro, G. G.*, Caprinellidae della Ciaca dei intorni di Palermo, 1865.—*Munier-Chalmas*, Prodrome d'une classification des Rudistes (Journ. de Conchyl. vol. XXI.), 1873.—*White, C. A.*, Bull. U.S. Geol. Surv., No. 4, 1884; No. 22, 1885.—*Douvillé, H.*, Bull. Soc. Géol. France [3], XIV. p. 389; XV. p. 756; XVI. p. 699; XVII. p. 627; XVIII. p. 324; XIX. p. 506; 1886-91.—*di Stefano, G.*, Studii stratigrafici e paleontologici sul systema cretaceo di Sicilia. I. Gli Strati con Caprotina. Palermo, 1888.—*Douvillé, H.*, Études sur les Rudistes (Mem. Soc. Géol. France. Paléontologie, I.-III.), 1890-93.

grotesquely distorted, sub-equal, with prolonged and twisted umbones, or the free valve is reduced to an opercular form, spiral, and even concave; the teeth often reversed relatively to their situation in Chama. Jura and Cretaceous.

Diceras, Lam. (*Heterodiceras*, *Plesiodiceras*, Mun.-Chalm.; *Pseudodiceras*, Gemm.) (Figs. 717, 718). Shell smooth, inequivalve, with both valves convex, the attached

Fig. 717.

Diceras arietinum, Lam. Coral-Rag; St. Mihiel, Meuse. 2/3.

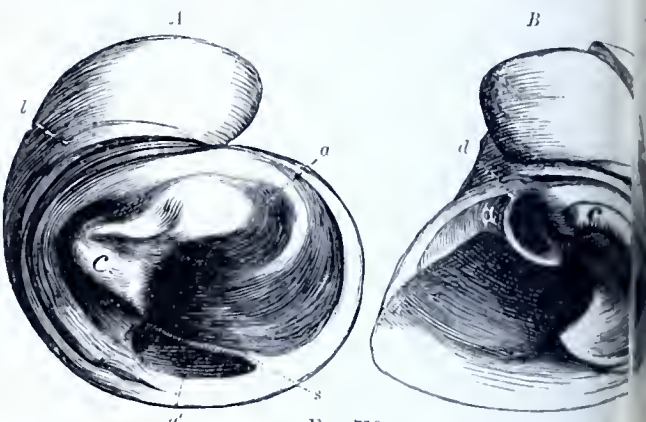


Fig. 718.

A, *Diceras arietinum*, Lam. Coral-Rag; St. Mihiel, Meuse, Fixed left valve, 2/3. *B*, *D. Zitteli*, Mun.-Chalm. Tithonian; Stramberg. Right valve, 2/3. *a*, *a'*, Anterior and posterior adductor scars; *c*, Major cardinal; *d*, Socket for left anterior cardinal; *l*, Ligamentary groove; *s*, Buttress ridge before posterior adductor scar.

valve larger, dentition normal or inverse; beaks prominent, prosocoelous; ligament as in *Chama*, supported on nymphae; right valve with a small anterior and large elongated curved posterior tooth almost parallel with the hinge margin; left valve

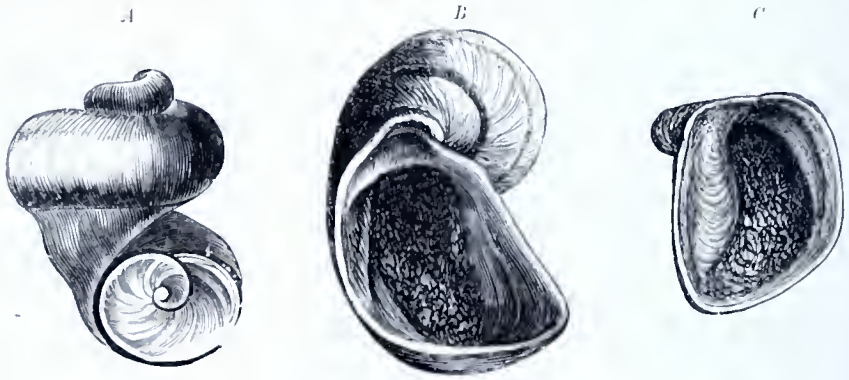


Fig. 719.

A, *Requienia ammonia*, Goldf. Urgonian; Orgon, Vaucluse. 1/3. *B*, *C*, Small individual of *R.* (*Toucasia*) *Lonsdalei*, Sow. sp., from same locality. *B*, Left; *C*, Right valve, 1/1.

with a single large ear-shaped tooth in front of the elongated socket for the principal tooth of the right valve; posterior adductor scar on a projecting buttress. Upper Jura.

Apricardia, Guéranger. Cenomanian and Turonian.

Requienia, Mathéron (Fig. 719, *A*). Smooth, very inequivalve, attached by the spirally twisted beak of the left valve; right valve opercular, spiral, flat; teeth feeble; posterior adductor scar buttressed. Lower Cretaceous, especially the Urgonian of Southern Europe, the Alps, and Texas.

Sub-genus *Toucasia*, Mun.-Chalm. (Fig. 719, *B*, *C*). Differs from *Requienia* in having both valves keeled. Urgonian and Cenomanian.

Matheronia, Mun.-Chalm. Urgonian and Cenomanian.

Family 11. **Monopleuridae.** Fischer.

Shell substance without canals; shell sessile, closed, very inequivalve; free valve with the cardinal formula 101, *operculiform or slightly spiral; fixed valve with the formula* 010, *conical, unrolled, or spiral; area wanting; ligament external, parivincular, opisthodetic.* Cretaceous.

Monopleura, Math. (*? Dipilidia*, Math.), (Figs. 720, 721). Very inequivalve, smooth or ribbed; dentition always inverse; attached by the right valve, which may be either

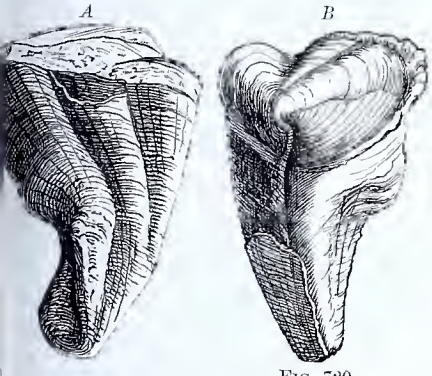


Fig. 720.

Monopleura trilobita, d'Orb. Neocomian (Schrattenkalk); Orgon, Vaucluse. 1/1. *A*, *B*, Anterior and posterior views. *C*, Interior of attached valve.

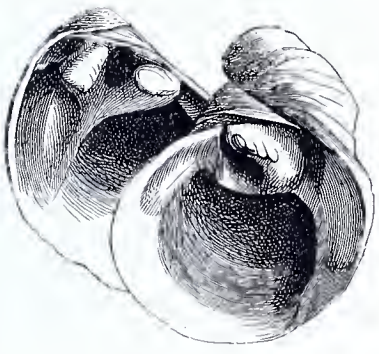


Fig. 721.

Monopleura varians, Math. Urgonian; Orgon, Vaucluse. Interior of both valves. 1/1.

twisted or coniform; left valve conical or flat; ligament as in *Chama;* posterior adductor scar buttressed. Lower Cretaceous; Southern Europe and Texas.

Valletia, Mun.-Chalm. Neocomian. *Gyropleura*, Douvillé. Cenomanian to Senonian. *Bayleia*, Mun.-Chalm. Turonian. *B. Pouechi*, Mun.-Chalm.

Family 12. **Caprinidae.** D'Orbigny.

Shell substance internally furnished with large parallel canals, the external layer prismatic; valves heavy, irregular, unequal, closed; free valve spiral, cardinal formula

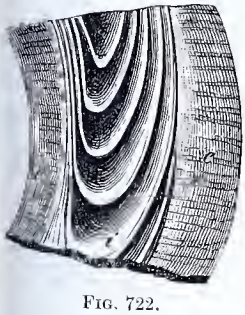


Fig. 722.

Longitudinal section of the fixed valve of *Caprina adversa*, showing cavities in the inner shell layer.

Fig. 723.

Cross-section of the free valve of *Caprina communis*, showing parallel canals in the middle layer.

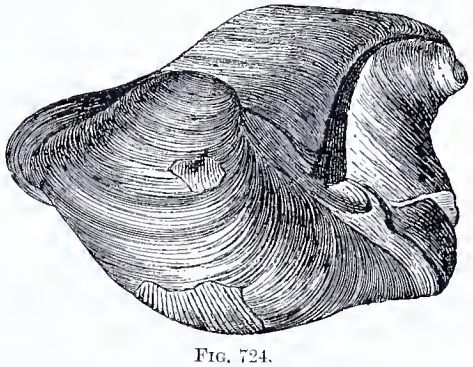


Fig. 724.

Plagioptychus Aguilloni, d'Orb. Upper Cretaceous; Gosau, Austria. 2/3.

101, *with a posterior myophoric crest for the adductor; fixed valve conical or spiral, cardinal formula* 010; *ligament in a deep groove, almost internal, parivincular, opisthodetic.* Cretaceous.

Caprina, d'Orb. (*Gemmellaria*, Mun.-Chalm.; *Cornucaprina*, Futt.), (Figs. 722, 723).

Very inequivalve, attached by the apex of the coniform right valve. Left valve large, spirally twisted; inner layer of lower valve made up of concentric lamellae between

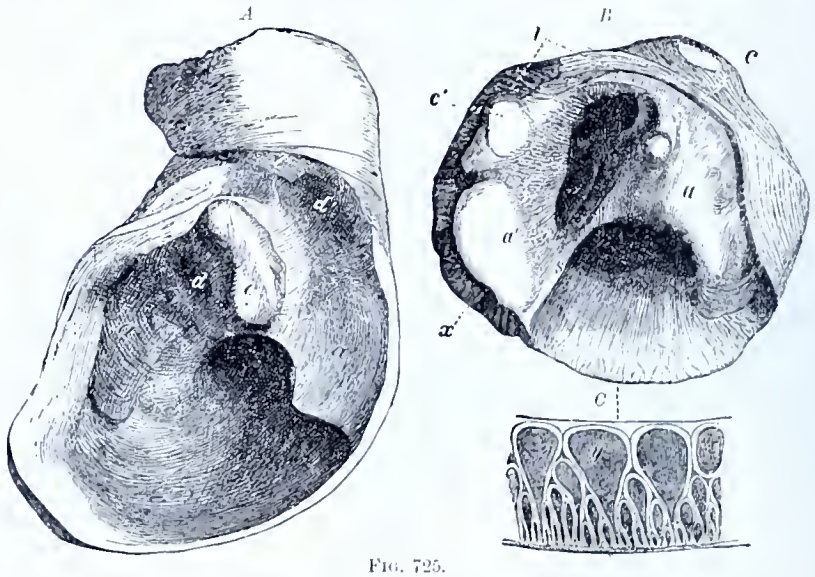


Fig. 725.

Plagioptychus Aguilloni, d'Orb. (*P. Coquandi*, Math.) Upper Cretaceous (Hippurites Limestone); Le Beausset, Var, France. *A*, Right. *B*, Left valve of the same individual, seen from within, 2/3. *a*, Anterior; *a'*, Posterior adductor scar; *l*, Ligamentary groove; *c*, Anterior tooth; *c'*, Posterior tooth of left valve; *d*, Socket; *s*, Buttress. *C*, Section of the small valve near the margin, showing canals (*y*) of the middle layer. Magnified.

which cavities are sometimes left. The middle layer of the free valve traversed by numerous simple, wide, parallel canals, extending from the margin to the apex; tooth of the attached valve well developed, a series of depressions between the posterior adductor scar and the margin. Cenomanian. The typical species, *C. adversa*, d'Orb., is of large size.

Schiosia, Böhm. Like *Caprina*, but the fixed valve

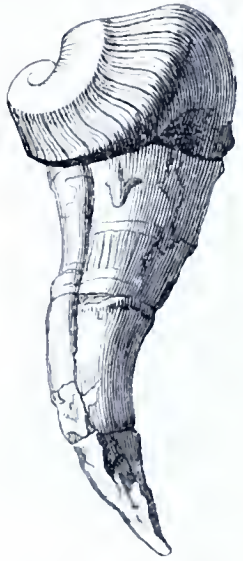


Fig. 726.

Caprinula Baylei, Gemm. Upper Cretaceous; Addauran, near Palermo. 1/2 (after Gemmellaro).

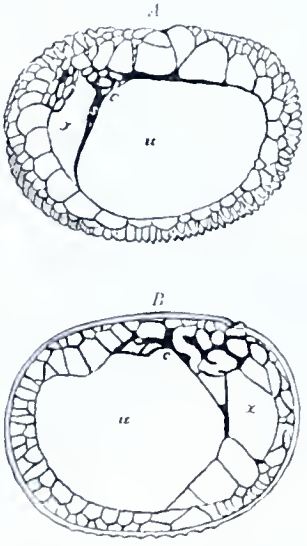


Fig. 727.

Caprinula Boissyi, d'Orb. Cross-section of the lower (*A*) and upper (*B*) valves. *c*, Teeth; *s*, Septum; *a*, Body cavity; *x*, Sockets. 2/3 (after Woodward).

Fig. 728.

Mass consisting of *Caprotina semistriata* and *C. striata*, d'Orb., and a smooth *Sphaerulites*. Greensand; Le Mans (after d'Orbigny).

somewhat gyrate and the canal system present in both valves. Cenomanian; Upper Italy.

Plagioptychus, Math. (*Sphaerucaprina*, Gemm.; *Orthoptychus*, Futt.), (Figs. 724,

725). Right valve conical or twisted, attached; left valve convex, with incurved beak; ligament as in *Chama*. Shell structure like *Caprina*, but the free valve with canals in the middle layer; the walls of the canals bifurcate outward, forming in section a fringe of peripheral minor channels (Fig. 725, *C*). Cenomanian and Turonian.

Caprinula, d'Orb. (*Chaperia*, Mun.-Chalm.), (Figs. 726, 727). Right valve elongated, attached, conical, or incurved; left smaller, gyrate; both with canal system, the peripheral canals smaller; hinge as in *Caprina*. Cenomanian and Turonian, especially in Portugal, Sicily, and Texas.

? Ichthyosarcolites, Desm. (*Caprinella*, d'Orb.) Cretaceous. *Caprotina*, d'Orb. (Fig. 728). Canals obsolete, replaced in some species by cavities. Neocomian to Turonian.

Coralliochama, White. Right valve conical, elongated, attached; left smaller, with incurved beak; anterior cardinal tooth buttressed, strong; posterior cardinal weak; canals as in *Plagioptychus*, bounded within by a coarsely cellular layer; lower valve with a prismatic outer and laminar inner layer, separated by an intermediate cellular stratum. Cretaceous; California.

Superfamily 6. RUDISTAE. Lamarck.

Chamacea in which the spirality of the valves has been lost, the area and ligament vertically submerged, and the dorsal margins recurved over them so as to bring the ligament into a sub-central position above the teeth but far below the dorsal margin, where it finally becomes obsolete. The teeth, no longer forming a hinge but rather a clithrum, specially modified for the vertical motion of the operculiform left valve, in which rotation is prevented by the projection of the modified teeth into deep sockets in the fixed valve; the latter conical, thick; pallial line simple, enclosing the whole cavity; shell structure specialised in two very different layers; sessile, marine.

The prisms of the outer shell layer are parallel to the long axis of the valve, and are cut at right angles by numerous tabulae, which, together with the upper margin, often bear impressions of radial vessels. The laminae of which the inner layer is composed are often separated by cavities which recall the septa of Cyathophylloid corals, or those cavities found in some oyster shells. In *Hippurites* the outer layer is traversed by a complex of canals. The *Rudistae* are the most peculiarly modified of all Pelecypods. Their relationship to the *Chamidae* through *Monopleura* and *Caprotina* was first recognised by Quenstedt, and afterwards confirmed by Woodward, Bayle, Zittel, Munier-Chalmas, Douvillé, and others. Formerly the group was referred to the most diverse connections, such as Brachiopods, Corals, Cirripedes, etc., or placed in a special class by itself.

The majority of Rudistids occur gregariously in large numbers, sometimes filling entire beds; they are often found in their natural position, standing vertically on the apex of the attached valve. Notwithstanding their abundance, it is extremely difficult and often impossible to separate the two valves and expose the interior, hence the hinge of many species is still only imperfectly known.

Family 13. Radiolitidae. Gray (emend.)

Shell substance with the external layer thick, prismatic; the internal thin, cellulo-crystalline (frequently destroyed in fossilisation); valves very unequal, the ligamentary subsidence usually marked; free valves with two projections and two somewhat irregular myophores; fixed valve with one myophore and two sockets; summit of the valves sub-marginal in the young, sub-central in the adult. Cretaceous.

Radiolites (Lam.), Bayle (*Biradiolites*, d'Orb.), (Fig. 729). Lower valve conical, erect, elongated, vertically ribbed, or made up of successive layers; usually with two somewhat smooth bands extending from the apex to the upper margin, which are supposed by Douvillé to indicate the position of siphonal orifices; outer layer very thick, composed of large polygonal cells or hollow prisms (Fig. 731). Upper valve operculate, flat, or conical, with central or eccentric umbo. *Clithrum* formed by

two vertically projecting striated processes (Fig. 729, *c*, *c'*), fitting into sockets near

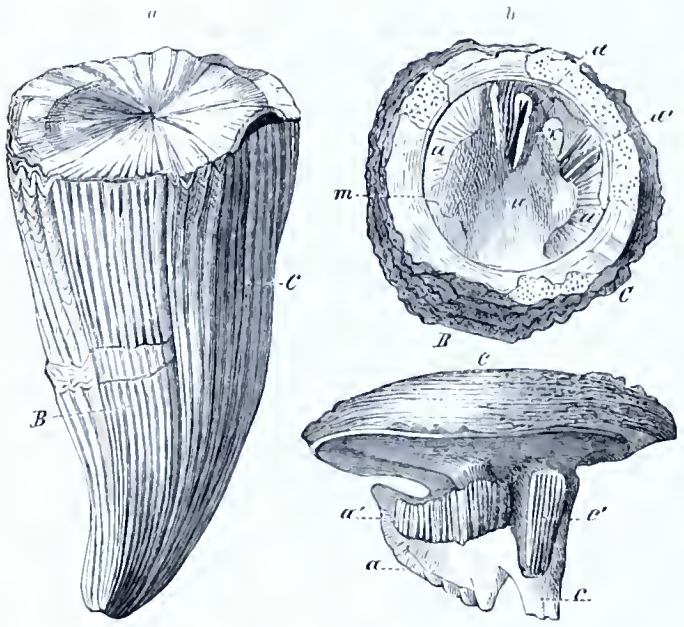


Fig. 729.

a, *b*, *Radiolites* (*Biradiolites*) *cornu-pastoris*, d'Orb. Middle Cretaceous (Carentonian); Pyles, near Périgeux. *a*, Shell with closed valves. *B*, *C*, The two more finely ribbed vertical bands. *b*, Interior of larger valve, viewed from above. *a*, *a'*, Adductor scars; *m*, Pallial line; *x*, Space occupied by soft parts; *s*, Empty space between the sockets. 1/2 (after Bayle). *c*, Opercular valve of *R. Bournoni*, Desm. sp. Upper Cretaceous (Dordonian); St. Mametz, Dordogne. *a*, Anterior; *a'*, Posterior myophore; *c*, *c'*, Anterior and posterior processes of clithrum. 1/3 (after Bayle).

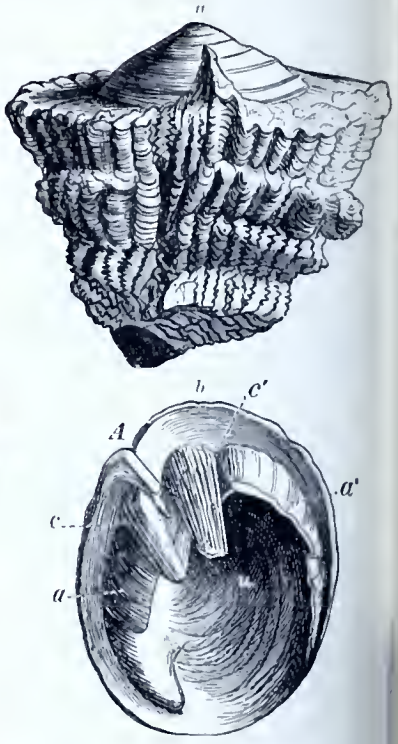


Fig. 730.

Sphaerulites angeiodes, Lam. Upper Cretaceous; Gosau, Austria. *a*, Shell with closed valves, 1/1. *b*, Opercular valve, 1/1. *A*, Sinus of hinge. *a*, *a'*, Myophores; *c*, *c'*, Processes of clithrum.

the outer wall of the fixed valve; next to and outside of the sockets are two large unequal slightly excavated adductor scars, corresponding to two broad myophores in the upper valve. Middle and Upper Cretaceous; Europe and Texas.

Sub-genera: *Lapeirousia*, Bayle. The smooth bands correspond internally to two prominent tubercles. *Synodontites*, Pirona. Has the two teeth of the upper valve fused.

Sphaerulites, Delam. (*Radiolites*, *Birostrites*, Lam.; *Jodamia*, Defr.; *Dipilidia*, *? Agria*, Math.), (Figs. 730-732). Externally like *Radiolites*, but without the two bands; valves with a re-entrant sinus between the teeth, which fit into separate pits (*d*, *d'*), usually joined by a ridge with the inner margin of the sinus; the two

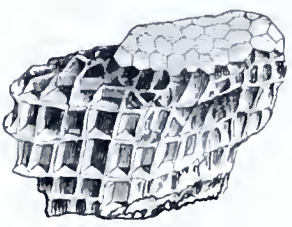


Fig. 731.

Portion of the outer shell layer of the lower valve of a *Sphaerulites* or *Radiolites* showing the large hollow prisms. Cretaceous; Monte Gargano, Italy. 1/1.

Fig. 732.

Sphaerulites foliaceus, Lam. Carentonian; Ile d'Aix, Charente. *A*, Sinus of the hinge. *a*, *a'*, Anterior and posterior adductor scars; *d*, *d'*, Anterior and posterior grooved sockets for the processes of the upper valve; *x*, *x'*, Empty spaces of the ligament pits; *y*, Cavity at the inner end of the sinus. 2/3 (after Goldfuss).

depressions (Fig. 732, *x*, *x'*) next the sinus were shown by Pethö to have been the seat of a ligmentary connection between the valves; the adductor scars (*a*, *a'*) resemble those of *Radiolites*. Widely distributed in the Middle and Upper Cretaceous.

The supposed genera *Dipilidia*, *Birostrites*, and *Jodamia* are based on internal casts of *Radiolites*. The visible submersion of the ligament in some *Radiolites* enables us to understand how the stages shown by *Hippurites* have arisen.

Family 14. **Hippuritidae**. Gray.

Shell substance of two layers, the external porous, grooved, and punctate; the inner lacunary and prismatic; exterior with sutures corresponding to an "anal" and "branchial" inflection, and sometimes with a ligamentary suture; clithrum formed of two processes in the free valve, the adductors attached to myophores; fixed valve with one thin laminar process; the adductor scars excavated, the anterior adductor duplex, forming distinct scars. Cretaceous.

Hippurites, Lam. (Figs. 733-737). Lower valve cylindro-conic, sometimes a metre in length, attached by the apex, smooth or longitudinally ribbed, with three furrows

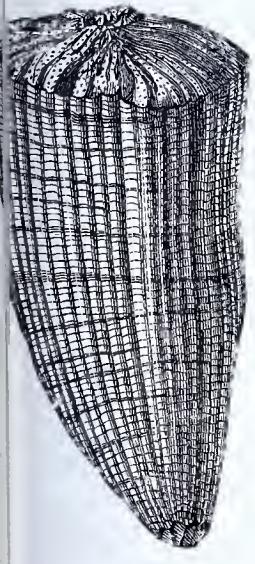


Fig. 733.

Hippurites Gosaviensis, Douv. Upper Cretaceous; Gosau Valley, Austria. 1/2.

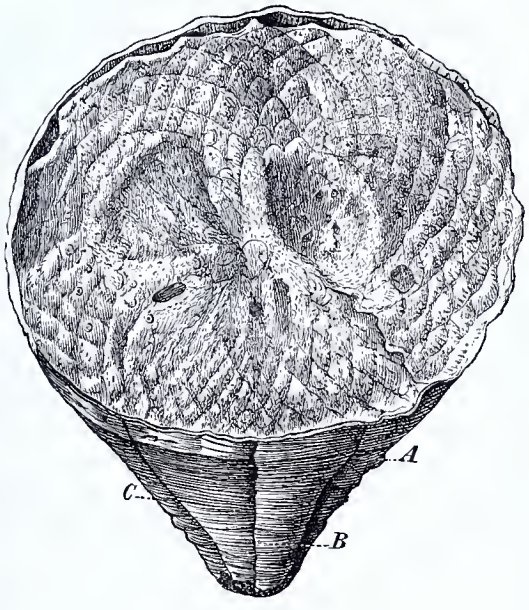


Fig. 734.

Hippurites Oppeli, Douvillé. Nefgraben, near Russbach, Salzburg. *A*, *B*, *C*, Impressed lines bounding convex vertical areas (columns) corresponding to the region of the hinge. 1/2.

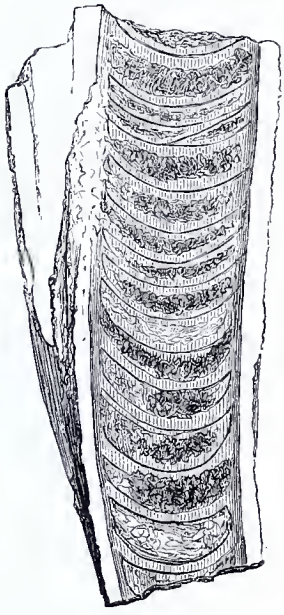


Fig. 735.

Hippurites organisans, Montf. Vertical section of a valve below the living chamber, showing the septa and interseptal cavities of the middle layer. 1/1.

bounding two "columns," or columnar areas, extending from the apex to the upper margin (*A*, *B*, *C*). Upper valve depressed, conic, with sub-central umbo, usually with two round or oval foramina; outer surface showing pores, the apertures of short canals which join larger canals radiating from the beak. The thick outer layer of the lower valve is usually brown-coloured and made up of thin horizontal strata, which are in turn composed of small vertical prisms. The white inner layer is porcellanous, and sometimes contains vacant spaces in the lower part of the shell. Three prominent folds are present, on the inner side of the shell, formed by the inbending of both layers of shell, and corresponding to the external grooves (*A*, *B*, *C*). Of these the

anterior (*A*) is longer and thinner than the others, which are thickened at the internal end and carry a small tubercle above. In the two sub-genera, *d'Orbignyia*, Woodward

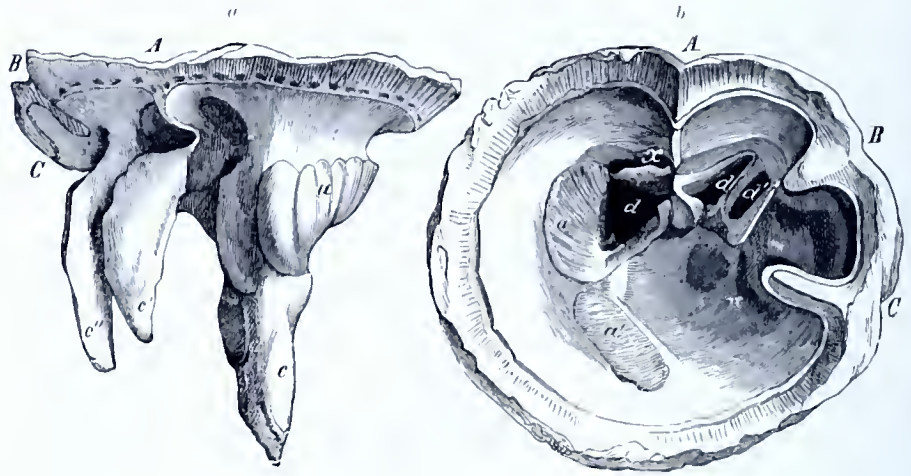


Fig. 736.

Hippurites radiosus, Desm. Upper Cretaceous (Dordonian); Royan, Charente. *a*, Upper valve (*A*, Sinus of the hinge; *B*, *C*, Grooves corresponding to anterior and posterior columns of the lower valve; *c*, Anterior, and *c'*, *c''*, Posterior processes of the clithrum). *b*, Interior of lower valve seen from above (*A*, Sinus; *B*, *C*, Position of anterior and posterior columns; *a*, *a'*, Adductor scars; *d*, Socket of anterior, and *d'*, *d''*, of posterior processes of clithrum; *v*, Body chamber of shell; *x*, Vacant cavity near the sinus). 2/3 (after Bayle).

(*H. biloculus*, Lam.), and *Batolites*, Montfort (*H. organisans*, Lap.), the anterior sinus disappears entirely. In *Pironaia*, Menegh., a number of accessory folds appear behind the two columns. According to Douvillé, the two posterior columns are homologous with the smooth bands of *Radiolites*, and indicate the position of the siphons. Woodward supposes that the pit (*x*) contained the internal ligament; but so far, remains of the ligament have only been found in the bottom of the outer anterior sulcus, where it seemed to form a vertical band. The second adductor scar is small, and located between the sulcus and the anterior column (*B*). The clithrum of the upper valve is extremely difficult to prepare, and is known in only a few species. The anterior process shows near its base two tubercles (*a*, *a'*), which correspond to the divided adductor scar of the lower valve. Behind the anterior there are two supplemental processes, which are received into the sockets *d'* and *d''* of the lower valve. The species are very abundant in the Middle and Upper Cretaceous, and occur chiefly in littoral shallow water deposits. The most noted localities are the Alps and Pyrenees, Provence, Charente, Istria, Dalmatia, Greece, Sicily, Asia Minor, Persia, and Algiers.

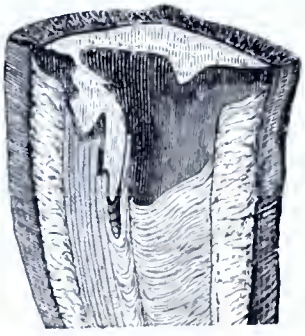


Fig. 737.

Hippurites cornu-vaccinum, Goldf. Upper Cretaceous; Gosau, Austria. Vertical section through both valves showing the interlocking clithrum and relation of the shell-layers. 1/2.

Barrettia, Woodward. Cretaceous; Jamaica and Guatemala.

Superfamily 7. LUCINACEA. Anton (emend.)

Shell with the anterior adductor scar narrower, produced ventrally; posterior scar shorter, rounded; pallial line simple; foot elongate, sub-clavate; hinge feeble, teeth radial, often obsolete.

Family 15. **Tancrediidae.** Fischer.

Shell Donaciform, equivalve, with an external ligament; the margin of the valves entire; hinge with posterior and anterior laterals, the latter inconstant; cardinals one in the left or two in the right valve, or two in each valve. Trias and Cretaceous, ? Recent.

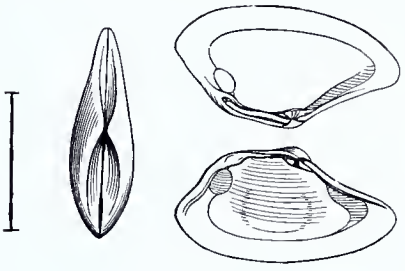


Fig. 738.

Tancredia securiformis, Dunker sp. Lower Lias; Hettingen, Lorraine. 1/1 (after Terquem).

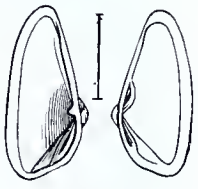


Fig. 739.

Tancredia (Palaeomya) corallina, Zitt. and Goub. Coral-Rag; Glos, Calvados.

Tancredia, Lycett (*Hettangia*, Terq.; *Palaeomya*, Zitt. and Goub), (Figs. 737, 738). Shell sub-arcuate, attenuated before the beaks, wider and shorter behind them; obliquely truncate and somewhat gaping posteriorly; a cardinal tooth on each side, and also an elongated posterior lateral. Trias to Cretaceous; maximum in Lias.

? *Meekia*, Gabb. Cretaceous; California. ? *Hemidonax*, Mörch (*Donacicardium*, Vest). Recent.

Family 16. **Unicardiidae.** Fischer.

Shell cordiform, equivalve, closed, concentrically striated; adductor scars elliptical, the anterior longer; pallial line simple; margin of the valve smooth; ligament external, parivincular, seated in a groove; with a grooved hinge plate bearing a single obsolete cardinal in each valve, or none. Carboniferous to Cretaceous.

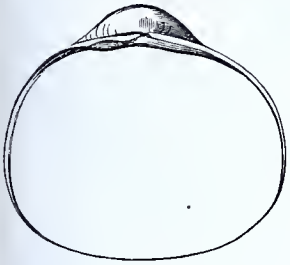


Fig. 740.

Unicardium excentricum, d'Orb. Kimmeridgian; Cap de la Hève, near Havre. 1/1.

Unicardium, d'Orb. (Fig. 740). Rounded, inflated, with incurved beaks; hinge margin thin, with a weak cardinal tooth; ligament deep-seated. Trias to Cretaceous.

Scaldia, Ryckholt. Carboniferous.

Pseudedmondia, Fischer. Ligament completely external. Carboniferous.

Family 17. **Lucinidae.** Fleming.

Shell substance porcellanous or chalky, usually with inconspicuous or dehiscent epidermis, rounded, variably sculptured; valves equal, free, closed, with low, prosocoelous beaks; adductor and pedal scars adjacent or distinct, the latter small; anterior adductor elongated, largely within the pallial line, which is not sinuate; area within the pallial line often granular or punctate; cardinal area small, often deeply impressed; ligament and resilium sub-internal, set in a deep groove, but usually more or less visible externally; hinge plate distinct; lateral laminae distant from the cardinals, anterior and posterior in the right, with corresponding sockets in the left valve; cardinal teeth radial, formula $\frac{\text{L1010}}{\text{R0101}}$, *the posterior tooth larger and often bifid, but any or all of the teeth may be obsolete or absent.* Silurian to Recent.

Paracyclas, Hall. Rounded, thin-shelled, concentrically striated; no lunule; hinge unknown. Devonian.

Lucina, Brug. (Figs. 741-744). Rounded, convex, or lenticular, usually with a

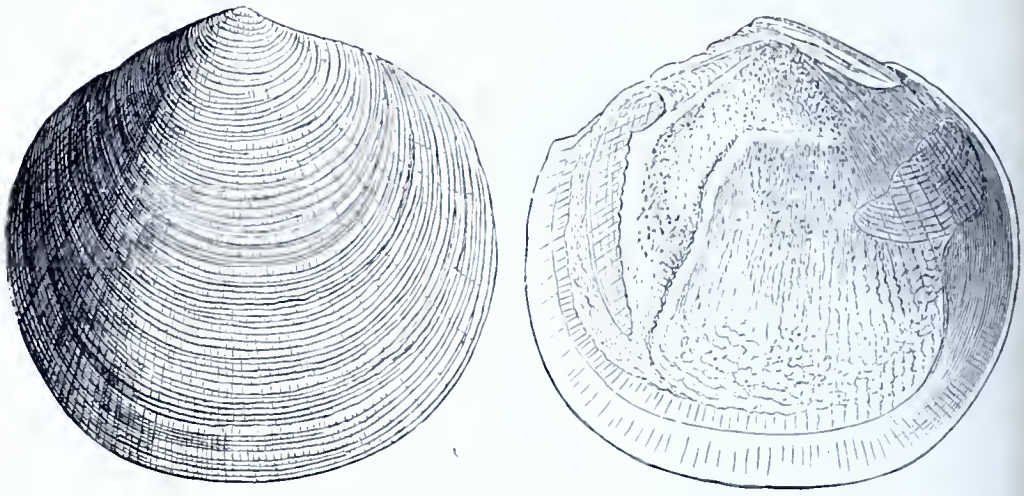


Fig. 741.

Lucina (*Miltha*) *gigantea*, Desh. Eocene (Calcaire Grossier); Grignon, near Paris. 2/3.

lunule; with delicate, concentric, or more rarely radial sculpture; dentition usually

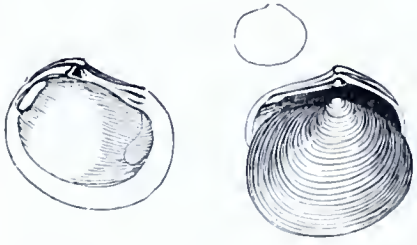


Fig. 742.

Lucina pulchra, Zitt. and Goub. Coral-Rag; Glos, Calvados. 2/1.

Fig. 743.

Lucina (*Prolucina*) *prisca*, His. Silurian; Gottland. Internal cast (after Roemer).

normal, the laterals developed. Represented by upwards of 300 fossil and 100 recent species. ? Silurian, Trias to Recent.

Sub-genera: *Lucina* s.s., Lam. 1799 (*Loripes*, auct.) Shell smooth. Adult with the teeth and posterior radial plication of the valves obsolete. Tertiary and Recent.

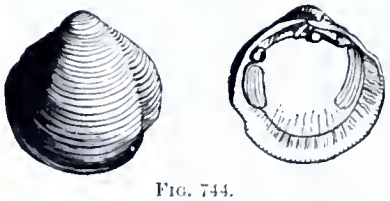


Fig. 744.

Lucina (*Myrtea*) *columbella*, Lam. Miocene; Steinabrunn, near Vienna.

Prolucina, Dall (Fig. 743). Compressed, arcuate, almost rostrate; the anterior side larger. Silurian.

Myrtea, Turton (Fig. 744). Rounded, sub-equilateral; teeth and posterior fold present. Tertiary and Recent.

Codakia, Seopoli. Compressed, reticulately sculptured. Tertiary and Recent.

Miltha, Adams. (Fig. 741). Compressed, nearly smooth; laterals absent, cardinals long, feeble (3. 2). Tertiary and Recent.

Divaricella, Martens. Rounded, inflated, valves ornamented with angular divergent grooving. Tertiary and Recent.

Family 18. **Corbidae.** Dall.

Shell differing from the Lucinidae in being transversely oval, thick, with a heavy hinge plate, and usually well-developed laterals; two or three strong cardinals in each valve; the margin of the valves denticulate, and the exterior strongly sculptured; ligament external, the adductor scars oval, and not projecting into the pallial area. Trias to Recent.

This family is an offshoot of the *Lucinidae*, with which it is commonly united.

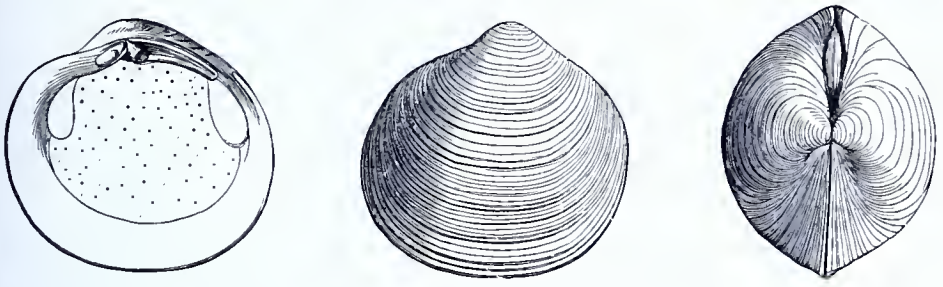


Fig. 745.

Gonodon Mellingi, Hauer. Upper Trias; Sarize am Predil, near Raibl, Tyrol. 1/1.

Gonodon, Schafh. (*Corbis*, p. p. auct.), (Fig. 745). Rounded, plump, concentrically striated. Cardinals $\frac{\text{L101}}{\text{R010}}$; sometimes a weak posterior lateral present. Trias and Jura.

Corbis, Cuv. (*Fimbria*, Megerle non Boh.), (Fig. 746). Thick-shelled, oval, inflated, reticulately sculptured; each valve with two short cardinals, and anterior and posterior laterals: adductor scars similar, sub-equal. Jura to Recent.

Sphaera, Sow. (*Palaeocorbis*, Conr.) Lower Cretaceous. *Sphaeriola*, Stol. Trias to Cretaceous. *Fimbriella*, Stol. Chalk of Britain. *Corbiccla*, Mor. and Lyc. Jura.

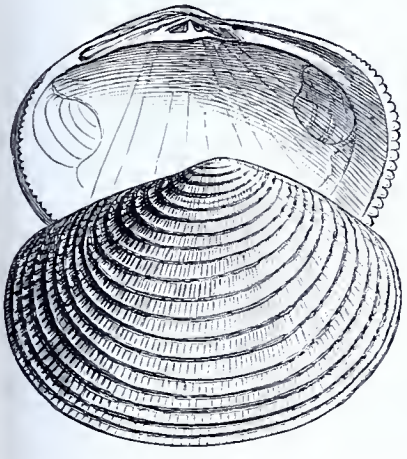


Fig. 746.

Corbis lamellosa, Lam. Eocene (Calcaire Grossier); Grignon, near Paris. 1/1.

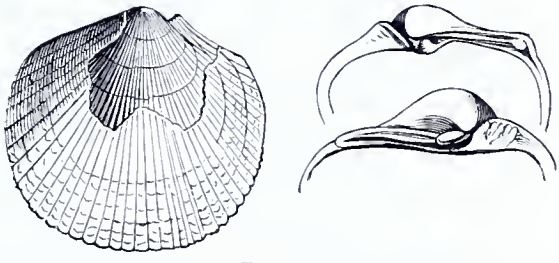


Fig. 747.

Mutiella coarctata, Zitt. Turonian; Gosau, Austria. 1/1.

Mutiella, Stol. (Fig. 747). Anterior cardinal border corrugated, upturned; posterior rectilinear, horizontal, with a feeble lateral tooth. Upper Cretaceous.

Family 19. **Diplodontidae.** Dall.

Shell sub-circular in outline, rarely nestling and irregular; hinge with the laterals obscure or absent, and the valve margins plain; the adductor scars continuous peripherally with the pallial line; soft parts like the Lucinidae, but with the external limb of the gills developed, and the anal foramen not tubular. ? Jura, Cretaceous to Recent.

Diplodonta, Bronn (Fig. 748). Thin-shelled, orbicular, convex, concentrically striate or pustulose; cardinals 2. 2, the left anterior and right posterior bifid; laterals obscure or absent. Tertiary and Recent.

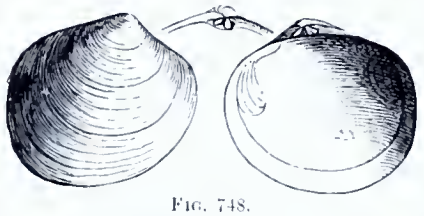


Fig. 748.

Diplodonta dilatata, Phill. Pliocene; Rhodes. 1/1.

Ungulina, Dandin. Nestling and often irregular. *Felania*, Récluz. Shell compressed; feeble laterals present. *Axinopsis*, Sars; *Sphaerella*, *Tenea*, Conrad. Cretaceous to Recent.

Family 20. **Cyrenellidae.** Fischer.

Shell as in Diplodonta, but with a conspicuous epidermis; pallial area smooth; pallial line not sinuate; hinge without lateral laminae; the cardinals like Diplodonta, or with two cardinals in each valve soldered to each other dorsally; cardinal formula $\frac{\text{L}010101}{\text{R}101010}$, *the anterior left cardinal usually obsolete.* Pliocene to Recent, in fresh or brackish water.

Cyrenoidea, Joannis (*Cyrenella*, Desh.) Pliocene of Florida, Recent in the Antilles and West Africa.

Joannisiella, Dall. Hinge as in *Diplodonta*, resilium immersed, the larger cardinal bifid, the teeth not soldered above. Cardinal formula $\frac{\text{L}1010}{\text{R}0101}$. Recent; Philippines.

Family 21. **Cryptodontidae.** Dall.

Shell substance earthy, with inconspicuous epidermis and prosocoelous beaks; valves equal, free, closed, with plain margins, smooth, or with feeble concentric striae, and usually with a radial posterior flexure; adductors Lucinoid, pallial area often punctate; ligament and resilium parivincular, opisthodetic, sub-external, seated in a groove; area impressed; hinge feeble without lateral laminae, edentulous, or with an obsolete cardinal tooth in the right valve. Cretaceous to Recent.

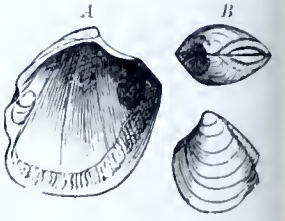


Fig. 749.

A, *Cryptodon sinuosus*, Don. Miocene; Grund, near Vienna. 1/1. *B*, *C. unicarinatus*, Nyst. Oligocene (Septaria-clay); Freienwalde, near Berlin.

Cryptodon, Turton (*? Axinus*, Sow.; *Conchocele*, Gabb), (Fig. 749). Smooth, thin-shelled, living in deep water. Cretaceous to Recent.

Philis, Fisch. Lunule deeply indented, projecting spoon-like into the cavity of the valves. Recent.

Superfamily 8. LEPTONACEA. Dall.

The incurrent and excurrent openings between the mantle lobes at opposite ends of the body, the former anterior.

This group contains a great many commensal, nestling, or parasitic forms; if independent usually very active, crawling like Gastropods on a sub-reptary foot, and with the mantle edges more or less reflected over the valves.

Family 22. **Leptonidae.** Dall.

Shell cellulo-crystalline with a periostraeum; valves equal, free, smooth-edged, often gaping, variably sculptured; adductor scars peripheral, sub-equal; pallial line simple; area obscure or none; ligament parivincular, opisthodetic, external, often obsolete; resilium usually internal, sub-umbonal or oblique; hinge plate narrow, channelled to receive the resilium; hinge variable, normally consisting of one or two radiating

cardinals and a pair of lateral laminae in each valve, the anterior laminae often absent, and the posterior frequently closely adjacent to the resilium, simulating cardinals. One Cretaceous, and a number of Tertiary and Recent species.

Erycina (Lam.), Fischer (Fig. 750); *Kellia*, Turton; *Pythina*, Hinds; *Lasea*, Leach; *Lepton*, Turton; *Erycinella*, Conrad; *Spaniodon*, Reuss; *Fabella*, Conrad., etc. Tertiary and Recent.

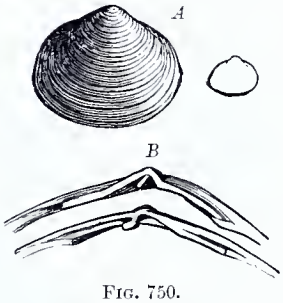


FIG. 750.

A, *Erycina pellucida*, Lam. Calcaire Grossier; Parnes. *B*, Hinge of *E. Foucardi*, Desh. Lower Eocene; Hérouval. Greatly enlarged (after Deshayes).

Family 23. **Galeommidae.** Gray.

Shell without a perceptible epidermis; valves equal, free, widely gaping ventrally, smooth, or variably sculptured; adductor scars distant, oval; pallial line simple; ligament usually obsolete, resilium internal, sub-umbonal, or oblique, attached to an excavated chondrophore in each valve; hinge plate hardly developed; laterals obscure or absent; one or two cardinal teeth in each valve or none. Tertiary and Recent.

FIG. 751.

Scintilla Parisiensis, Desh. Upper Eocene; Auvers, near Paris. $^2/_3$ (after Deshayes).

Scintilla, Desh. (Fig. 751); *Galeomma*, Turton; *Passyia*, *Sportella*, Desh.; *Hindsiella*, Stol.; *Ephippodonta*, Tate, etc. Tertiary and Recent.

Family 24. **Chlamydoconchidae.** Dall.

Shell cellulo-crystalline without an epidermis, comprising the prodissoconch with narrow, long laminar accretions, very small; valves wholly internal, not connected, contained in laterodorsal separate capsules, without hinge or hinge plate, not attached to muscles or ligament; ligament absent, resilium separately encapsuled between the obsolete valves, functionless. Recent; California.

The genus *Chlamydoconcha*, Dall, is evidently the last term in a series beginning with forms like *Lepton*, and continued by *Galeomma* and *Ephippodonta*, but the specialisation has been carried so far that it may well be regarded as the type of a distinct family.

Family 25. **Kelliellidae.** Fischer.

Shell with a periostracum; valves equal, free, closed, smooth externally with plain margins; pallial line simple; area obscure or none; ligament external, parivincular; resilium external or slightly sunken; hinge plate narrow, entire, with one or two cardinals, and a single anterior latcral placed above the anterior cardinal tooth. Tertiary and Recent.

Kelliella, Sars; *Lutetia*, Desh.; ?*Allopagus*, Stol.; *Turtonia*, Forbes. Eocene to Recent.

C. CYCLODONTA.

Teeth arched, springing from below the hinge margin, with the hinge plate obscure or absent.

Superfamily 9. **CARDIACEA.** Lamarck.

Lobes of the mantle free behind the siphons, foot elongate, geniculate; sculpture of the shell chiefly radial; cardinal teeth conical, the lateral laminae short, distant from the cardinals.

Family 26. **Cardiidae.** Fischer.

Shell substance cellulo-crystalline, with the external layer more or less tubular; valves equal, free, gaping slightly behind, the beaks prosocoelous, the margins usually serrate or radially striated; adductor scars sub-equal, the pedal distinct and usually distant; ligament and resilium parivincular, external, short, set in a groove; area obscure; complete hinge armature consisting of an anterior and posterior lateral in the left, and two

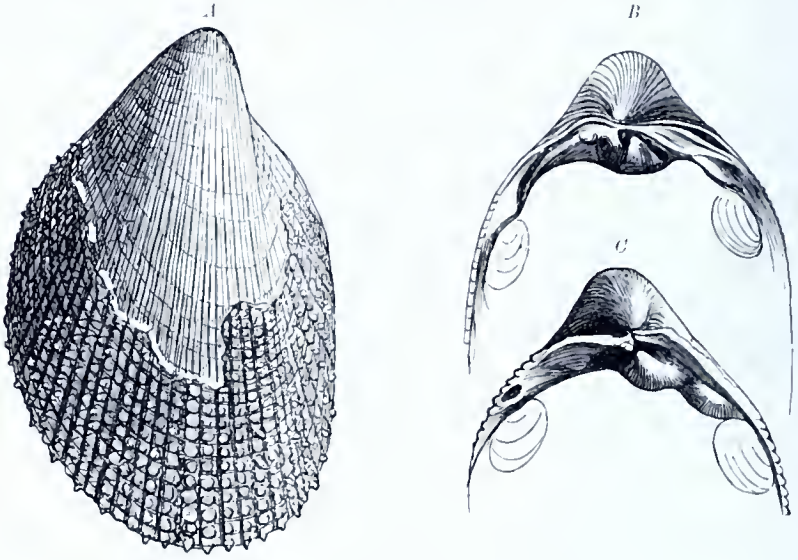


Fig. 752.

Cardium productum, Sow. Turonian; St. Gilgen, Salzburg. 1/1.

anterior and one posterior lateral in the right valve, any or all of which may be absent; cardinal formula $\frac{\text{L1010}}{\text{R0101}}$, *the teeth simple, smooth, never bifid, one cardinal in each valve usually persistent, the others inconstant.* Trias to Recent.

Cardium, Linn. (Figs. 752-754). Cordate, inflated, radiately ribbed or striated,

Fig. 753.

Protocardia bifrons, Reuss. Turonian; Strobl-Weissenbach am Wolfgangsee, Austria. 1/1.

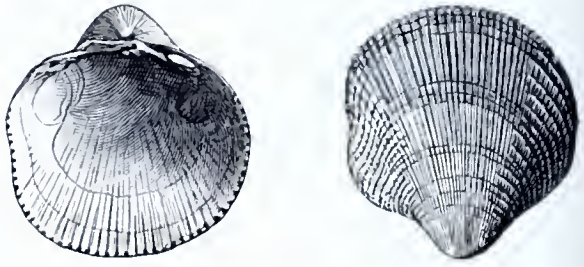


Fig. 754.

Cardium (*Discors*) *discrepans*, Bast. Miocene; Dax, near Bordeaux. 1/1.

with prominent beaks. Represented by about 200 recent and over 100 fossil species. Trias to Recent.

A very large number of sub-genera and sections have been proposed, based chiefly on the external sculpture. Some of the more conspicuous groups are the following:—

Protocardia, Beyr. (Fig. 753). Cretaceous. *Discors*, Desh. (Fig. 754); *Laevicardium*, Swains.; *Serripes*, Beck; *Hemicardium*, Cuvier; *Papyridea*, Swains. Tertiary and Recent. *Didacna*, Eichwald, estuarine, leads toward the next family.

Family 27. **Adacnidae.** Dall.

Like the Cardiidae, but thin-shelled, with long united siphons, a short compressed foot, a pallial sinus and obsolete hinge armature, living in brackish or fresh water. Tertiary and Recent.

Adaena, Eichw. Shell elongate oval, truncate behind, gaping at both extremities; siphons very long, pallial sinus deep. Miocene and Recent in Caspian Sea.

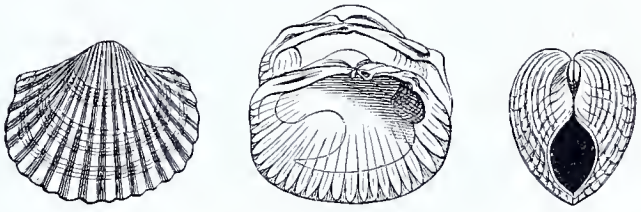


Fig. 755.

Limnocardium conjungens, Partsch. Pliocene (Congeria Stage); Brunn, near Vienna. 1/1.

Limnocardium, Stol. (Fig. 755). Cardinals weak, laterals strong, distant, pallial sinus moderate, shell closed anteriorly. In brackish Miocene beds, especially the Sarmatic and Pontic horizons of Eastern Europe, and in estuaries of the Aral, Black, and Caspian Seas.

Sub-genera: *Prosodacna*, Tourn. (*Psilodon*, Cob.); *Monodacna*, Eichw.; *Uniocardium*, Capell.; *Arcicardium*, Fischer.

Superfamily 10. TRIDACNACEA. Menke.

Soft parts rotated forward nearly 180° with relation to the valves as compared with normal Peleeypods, the anterior adductor wanting, and the posterior nearly central in the shell; cardinal teeth lamellar, oblique.

Family 28. **Tridacnidae.** Cuvier.

Shell very densely porcellanous, with no visible epidermis; valves equal free, with a byssal gape, radially sculptured, with serrate margins and prosocoelous beaks; ligament and resilium as in the Cardiidae; hinge with a single oblique cardinal in each valve, a single posterior lateral in the left, and two in the right valve. Eocene to Recent.

Byssocardium, Mun.-Chalm., and *Lithocardium*, Woodw., of the Eocene, are perhaps precursors of the recent *Tridaena*, Brug., and *Hippopus*, Lamarck.

Superfamily 11. ISOCARDIACEA. Dall.

Lobes of the mantle closed, except for the pedal and siphonal openings, smooth, double-edged; foot short, compressed; sculpture of the shell faint or concentric; cardinal teeth lamellar, parallel with the hinge margin.

Family 29. **Isocardiidae.** Gray.

Shell substance cellulo-crystalline, the external layer not tubulate, with a marked epidermis; valves equal, free, rotund, completely closed, with plain margins and prominent prosogyrous beaks; adductor scars sub-equal; pedal scar adjacent; area not distinctly limited; ligament and resilium external, parivincular, set in a deep groove, continuous to the beaks; complete armature of the hinge with an inconstant posterior lateral in each valve, and rarely, an anterior lateral close to the cardinals; cardinal formula $\frac{\text{L1010}}{\text{R0101}}$, *the teeth lamelliform, and very variable in details of form.* Jura to Recent.

Many species have been referred to this group solely on account of their having gyrate beaks. The Palaeozoic and many Mesozoic species so referred must be separated from *Isocardia*.

Isocardia, Lam. (Figs. 756, 757). Inflated, smooth, or concentrically striated; beaks distant, much produced, prosogyrate. Jura to Recent.

Fig. 756.

Isocardia striata, d'Orb. Portlandian; Cirey, Haute-Marne (after Loriol).

Meioeardia, Adams. Keeled, concentrically ribbed. Tertiary and Recent.
? Clisocolus, Gabb. Cretaceous; North America.

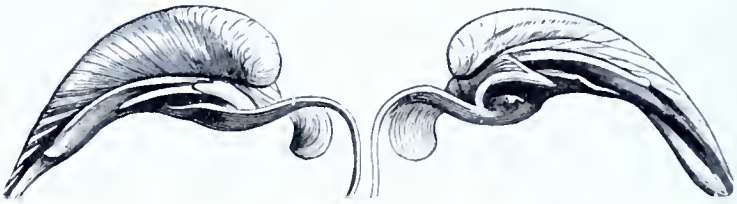


Fig. 757.

Hinge of *Isocardia lunulata*, Nyst. Crag; Antwerp.

Family 30. **Callocardiidae.** Dall.

Shell as in the Isocardiidae, but with low and inconspicuous beaks, the valves more elongated, and the lunule delimited by a sharp groove; cardinal formula $\frac{\text{L}010101}{\text{R}10\bar{1}010}$. Tertiary and Recent.

Callogonia, Dall. Pallial line deeply sinuated, and a distinct anterior lateral close to the cardinal teeth. Recent; abyssal.

Calloeardia, Adams. Rounded or Tapetiform, compressed, or not inflated, with low inconspicuous, non-gyrate beaks. Eocene and Recent.

D. Teleodonta.

The most perfected type of modern teeth, to which, in addition to the normal (10101) *cardinal series of the ordinary* Teleodesmacea, *there is added in the most specialised types* (Veneridae, Mactridae) *either a roughened area* (Venus), *a series of extra cardinals* (Tivela), *or accessory lamellae* (Mactra), *rendering the hinge more efficient, or complicated. The hinge characters of the less specialised forms hardly differ from the* Diogenodonta, *but they are grouped here on account of their obvious affinities, as shown by other characters.*

Superfamily 12. **VENERACEA.** Menke.

Teleodonts with normal gills united to form a complete anal chamber, the mantle lobes free behind the siphonal region, sub-equal adductors, an external parivincular ligament seated in a groove, and the shell substance densely cellulo-crystalline with inconspicuous epidermis. Complete hinge formula $\begin{matrix}\text{L}1l. & \times 0 \times 01010. & 1l \\ \text{R}2l. & \times 0 \times 010101. & 2l\end{matrix}$, *of which a large part is usually deficient.*

Family 31. **Veneridae.** Leach.

Valves equal, free, closed, with prosogyrous beaks, variably sculptured, with the margins more or less dentate, except in the smooth species; adductor scars peripheral, pedal distant; pallial sinus more or less sinuated, area very distinct; resilium usually external, embraced by the ligament; hinge plate developed; formula of the cardinals $\frac{\text{L}101010}{\text{R}010101}$*, with a single obsolete lateral in one valve; the cardinals frequently bifid, usually radially disposed and sub-equal in size, except the posterior left one, which is often obsolete or obscure; supplementary cardinals or rugosities are present in specialised forms.* Jura to Recent; maximum in Tertiary and later.

The family must be divided into at least four sub-families, as follows :—

a. Venerinae: typical, with produced siphons, not byssiferous, the young not retained within the mother after leaving the egg.

b. Circinae: with separate short siphons, correlative nearly simple parallel line, sub-internal, partially amphidetic resilium, and compressed beaks.

c. Tapetinae: with long but partly separated siphons, a byssus present at least in the young; hinge with no lateral teeth, otherwise like the *Venerinae*.

d. Gemminae: minute shells, with more or less separated siphons, no byssus, obsolete lateral laminae, and sheltering the nepionic young within the cavity of the mother.

Fig. 758.

Cyprimeria discus, Math. sp. Upper Cretaceous; Gosau Valley, Austria.

a. Pronoëlla, Fisch. (*Pronoë*, Ag. non Guér. Mén.) Compressed, pallial sinus very shallow; a posterior lateral and three cardinals in each valve. Jura.

Cyprimeria, Conr. (Fig. 758). Like the preceding, but the right valve with only two cardinals, the hinder one bifid; pallial sinus very shallow. Cretaceous.

Dosinia, Scop. (*Artemis*, auct.) Orbicular, lentiform, concentrically sculptured, with a deep, well-marked lunule; cardinals 3 : 3; pallial sinus deep, ascending, pointed. Cretaceous to Recent.

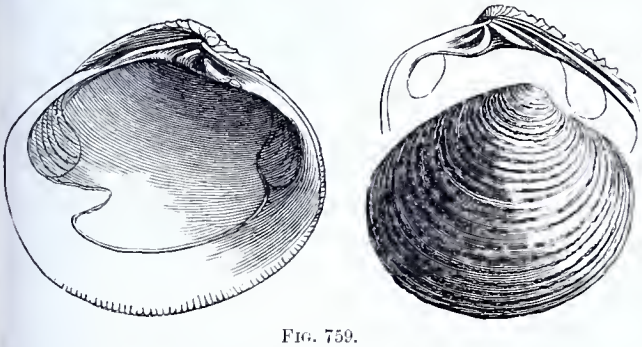


Fig. 759.

Venus cincta, Eichw. Miocene; Gainfahrn, near Vienna.

Cyclina, Desh. Cretaceous to Recent. *Sunetta*, Link (*Meroë*, Schum.); *Grateloupia*, Desm. Tertiary and Recent.

Venus, Linn. (Fig. 759). Oval or rounded, plump, cordate, thick; concentrically or radially sculptured, with denticulate margins; hinge plate broad, with three cardinals in each valve and no lateral teeth; pallial sinus short, angular. Jura to Recent; represented by about 200 fossil and as many recent species. Very numerous sub-divisions have been proposed; *Venus* s. s. is typified by *V. mercenaria*, Lam.

Meretrix, Lam. (*Cytherea*, auct.), (Figs. 760, 761). Hinge with lateral teeth. Tertiary and Recent.

Tivela, Link. Hinge with supplementary cardinals. Miocene to Recent.

Fig. 760.

Meretrix semisulcata, Lam. Eocene; Grignon, near Paris.

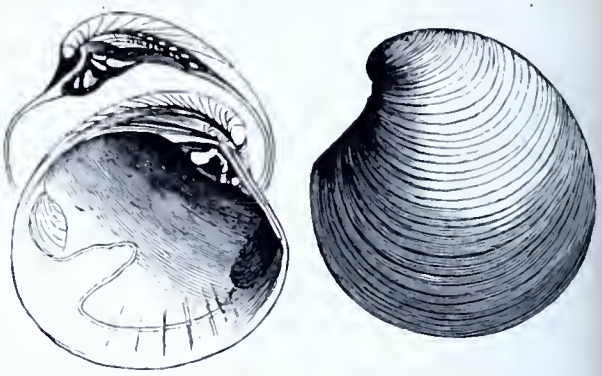


Fig. 761.

Meretrix incrassata, Sow. Oligocene; Weinheim, near Alzey.

b. Circe, Schum. (Fig. 762). Umbones compressed, sculpture often divaricate, ligament immersed. Tertiary and Recent.

Sub-genus *Gouldia*, Adams. Small, concentrically striated. Eocene to Recent.

Ptychomya, Agassiz. Cretaceous.

c. Tapes, Megerle (*Pullastra*, Sow.), (Fig. 763). More or less elongate, oval, with narrow hinge plate, divergent and often bifid cardinals, no laterals, and deep pallial sinus. Cretaceous to Recent; about 150 living species.

Fig. 762.

Circe eximia, Hoernes. Miocene; Enzesfeld, near Vienna.

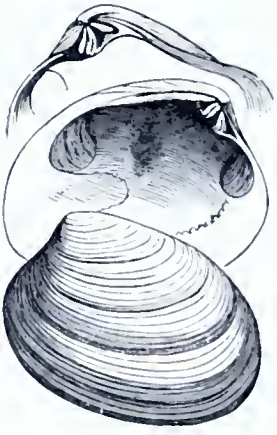


Fig. 763.

Tapes gregaria, Partsch. Sarmatian Stage; Wiesen, near Vienna.

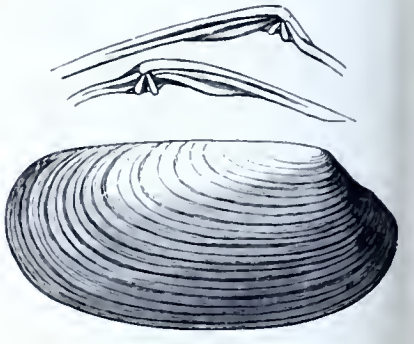


Fig. 764.

Tapes (*Baroda*) *fragilis*, d'Orb. sp. Upper Cretaceous; Gosau, Austria.

Of the numerous sub-genera *Baroda* (Fig. 764) and *Iscanotia* (Fig. 765), Stol., from the Cretaceous, are remarkable for their elongation and the ridge-like form of the posterior cardinal.

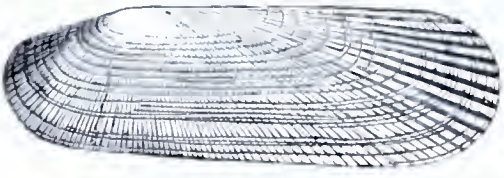


Fig. 765.

Tapes (*Iscanotia*) *impar*, Zitt. Upper Cretaceous; Gosau.

Oncophora, Rzehak. Differs from *Tapes* in having a very short pallial sinus, and the anterior adductor scar bounded by a ridge. Miocene brackish water-beds.

Venerupis, Lam. Cardinal teeth 2:2-3, strong; a borer or nestler, often deformed. Tertiary and Recent.

d. Gemma, Desh.; *Parastarte*, Conr.; *Psephis*, Carp. Minute shells. Eocene to Recent.

Family 32. **Petricolidae.** D'Orbigny.

Valves, when not distorted, equal, free, somewhat gaping behind, radiately sculptured with plain margins and inconspicuous beaks; posterior adductor scar larger than the anterior, pedal narrow, elongated, distinct; ligament and resilium external; area obscure or not defined; hinge without lateral laminae, with two or three small, usuall bifid, radial cardinal teeth in each valve. Cretaceous to Recent.

Petricola, Lam.; *Choristodon*, Jonas; and *Naranaio*, Gray, are the principal forms.

The family *Glaucomyaeidae*, of estuarine or fluviatile habit, appears to be related to *Petricola*, and includes the recent *Glaucomya* (Bronn), Woodward, and *Tanysiphon*, Benson.

Superfamily 13. TELLINACEA. Blainville.

Siphons distinct to their bases, usually long; pallial line sinuate; ligament external, seated on nymphs; hinge normally with an anterior and posterior lateral in each valve, two radial cardinals, of which the anterior is commonly bifid and somewhat pedunculated, and the posterior, as well as the laterals, often obsolete.

Family 33. **Tellinidae.** Deshayes.

Shell substance cellulo-crystalline, with an inconspicuous epidermis; valves slightly unequal, free, rounded in front, more or less rostrate, oblique, and gaping behind, compressed, usually with smooth margins, low beaks, and variable, chiefly concentric sculpture; anterior adductor scar larger, frequently irregular; pedal distinct; resilium embraced in the ligament, sub-external; area narrow, small, covered with a dark epidermis, or frequently obsolete; hinge plate narrow, anterior laterals approximate, posterior more distant from the cardinals, when present; cardinal teeth small; pallial sinus deep, discrepant in the opposite valves. Jura to Recent.

Fig. 766.

Tellina planata, Lam. Miocene; Pötzleinsdorf, near Vienna.

Fig. 767.

Tellina rostralina, Desh. Eocene Damery, near Epernay.

Fig. 768.

Tellina (*Lincaria*) *biradiata*, Zitt. Upper Cretaceous; Gosau, Austria.

Tellina, Linn. Elongated, the rostrum more or less twisted; two lateral teeth in each valve. Jura to Recent.

Sub-genera: *Tellina* s.s. (Figs. 766, 767), *Tellidora*, Mörch; *Strigilla*, Turton; *Lincaria*, Conr. (*Arcopagia*, d'Orb.), (Fig. 768), etc.

Macoma, Leach. Anal siphon long, branchial very short, hinge without laterals; shell smooth, less elongated than in *Tellina*. Tertiary and Recent.

Gastrana, Schum. (*Fragilia*, Desh.) Miocene and Recent.

Quenstedtia, Mor. and Lyc. Long, oval, obliquely truncate behind; beaks low, pallial sinus shallow, only a single cardinal tooth present. Jura.

Family 34. **Semelidae.** Dall.

Resembling the Tellinidae, but with the resilium internal, often on a distinct chondrophore, and with the laterals, when present, stronger and less distant. Tertiary to Recent.

Semele, Schum. (*Amphidesma*, Lam.) Shells large, rounded, thick, often conspicuously sculptured; 100 species. Tertiary and Recent.

Fig. 769.

Abra apelina, Ren. sp. Miocene; Grund, near Vienna.

Cumingia, Sow. Small, thin, with a spoon-like chondrophore; habit nestling. Tertiary and Recent.

Scrobicularia, Schum. Differs from *Semele* in having no lateral teeth. Tertiary and Recent.

Abra, Leach (*Syndosmya*, Récluz), (Fig. 769). Smooth, small, thin; cardinals 2 : 2, an anterior and posterior lateral present; chondrophore narrow, oblique, not separated from the hinge line. Tertiary and Recent; chiefly in deep water.

Family 35. **Psammobiidae.** Dall.

Shell as in the Tellinidae, *but usually more equivalve and less twisted, with more conspicuous epidermis and nymphs, broader hinge plate, and a wider posterior gape; lateral laminae on the hinge wanting, and the cardinals sometimes three in one valve; ligament external and conspicuous; no defined area.* Tertiary and Recent.

Psammobia, Lam. (*Gari*, Schum.), (Fig. 770). (?) Cretaceous. Tertiary and Recent.

Pliorhytis, Conrad; *Asaphis*, Modeer; *Sanguinolaria*, Lam.; and *Heterodonax*, Mörch. Tertiary and Recent.

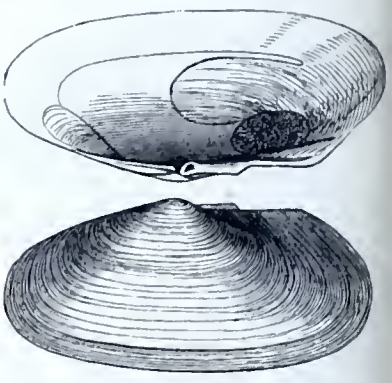


Fig. 770.

Psammobia effusa, Desh. Eocene (Calcaire Grossier); Parnes.

Family 36. **Donacidae.** Deshayes.

Valves equal, free, sub-trigonal, usually closed, solid; outer surface and inner margins smooth or radially sculptured, the posterior end usually shorter and obliquely sub-truncate; pallial sinus similar in both valves; resilium sub-internal, sometimes amphidetic; ligament short, external, seated in a deep groove, opisthodetic; hinge plate moderately developed, usually with a posterior and anterior lateral in the right, and corresponding sockets in the opposite valve; cardinal formula $\frac{\text{L}1010}{\text{R}0101}$, *the strongest cardinal tooth often bifid.* Lias to Recent.

The resilium is chiefly opisthodetic and sub-internal, but some of the large species have a small segment of the resilium separate from the rest, wholly internal, and in front of the beaks.

Isodonta, Buv. (*Sowerbya*, d'Orb.) Sub-symmetrical, convex, laterals strong, pallial sinus deep. Jura.

Donax, Linn. (Fig. 771). Anterior side longer, laterals weak. Upper Eocene and Recent; about 100 species. Sub-genus *Iphigenia*, Schum. Recent.

Egeria, Lea. Lower Eocene.

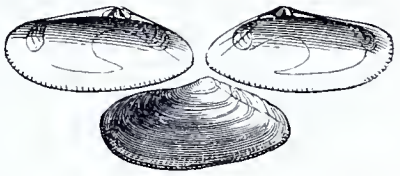


Fig. 771.

Donax lucida, Eichw. Miocene (Sarmatian Stage); Wiesen, near Vienna.

Superfamily 14. SOLENACEA. Lamarck (emend.)

Dwellers in soft sea-bottom, narrow, elongated, modified for burrowing, gaping at both ends; foot elongated, distally modified to serve as a piston or stilt within the burrow; hinge without lateral laminae.

Family 37. Solenidae. Leach.

Shell substance as in Tellina, but the external layer showing its cellular structure more clearly; with a pronounced epidermis; valves equal, free, usually truncate at both ends, and more or less inequilateral, with low beaks, smooth margins, not rostrate, smooth or feebly sculptured; adductor scars narrow, elongate, dorsally distributed, pedal distinct; pallial sinus small in species with anterior umbones, and vice versa; ligament and resilium external, parivincular, seated on nymphs; area obscure or none; hinge plate hardly developed; hinge often with a thickened ray crossing the valves and serving as a buttress; cardinals varying from one to four in each valve, usually a single slender radial laminar cardinal in the right, and two in the left valve, with or without one or two placed parallel with the hinge margin, simulating laterals; radial teeth usually more or less pedunculated, rarely bifid. Devonian to Recent.

The Silurian forms heretofore referred to this family do not seem to belong to it, but *Palaeosolen*, Hall, is scarcely distinguishable externally from some modern forms; its hinge,

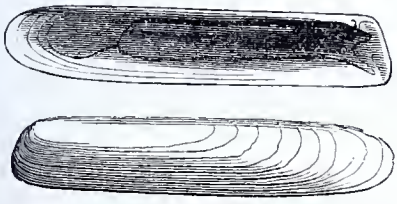


Fig. 772.

Solen subfragilis, Eichw. Miocene (Sarmatian Stage); Pullendorf, Hungary.

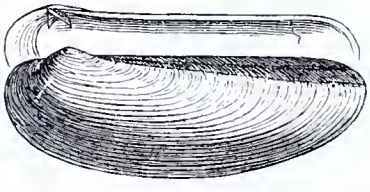


Fig. 773.

Cultellus Grignonensis, Desh. Calcaire Grossier; Grignon, near Paris.

however, is unknown. The species of this family are mostly much modified for a special mode of life, hence the variability in certain features, such as the siphons, foot, and fermature of the mantle lobes. *Novaculina* has been naturalised in fresh water, and *Tagelus* appears to prefer estuaries.

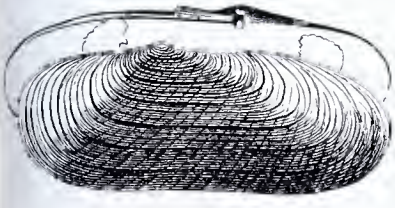


Fig. 774.

Solecurtus (*Macha*) *Deshayesii*, Desm. Calcaire Grossier; Grignon, near Paris. 1/1.

Solen, Linn. (Fig. 772). Scabbard-shaped, straight, with terminal beaks. Among the numerous sub-genera are: *Ensis*, Schum.; *Pharella*, Gray; *Ceratisolen*, Forbes; *Siliqua*, Megerle; *Cultellus*, Schum. (Fig. 773). Tertiary and Recent.

Palaeosolen, Hall. Devonian. *Leptosolen*, Conrad. Cretaceous.

Solecurtus, Blainv. (*Psammosolen*, Risso). Cretaceous to Recent. Sub-genera: *Macha*, Oken (Fig. 774); *Tagelus*, Gray; *Novaculina*, Benson, fresh water.

Superfamily 15. MACTRACEA. Gray.

Resilium internal, seated on chondrophores, left cardinal tooth bifid, fitting below the two right cardinals, which are more or less joined together dorsally. Inner wall of the mantle behind the siphons exhibiting a laminar sense organ.

Family 38. Mactridae. Gray.

Shell porcellanous, with an obvious epidermis, usually rounded-triangular, with smooth or concentrically sculptured surface, smooth margins, and prominent prosogyrous beaks; valves equal, free, usually with a slight posterior gape; area not limited; ligament variably external or internal; resilium connecting sub-triangular chondrophores usually excavated out of the hinge plate, rarely with a prop or buttress; hinge plate well developed, with normally an anterior and posterior lateral in the left, received into sockets or paired laminae in the right valve, or obsolete; cardinals in the right valve two, with their dorsal edges usually soldered together, and one bifid or deltoid cardinal in the left, fitting below the former, a delicate accessory lamella often present in either valve, or all may be more or less obsolete; siphons well developed, united, and usually with an epidermal tunic; adductors peripheral, sub-equal. Cretaceous to Recent.

This group is so large and its extremes so variable, that it is best divided into sub-families, as follows:[1]—*Mactrinae*, *Pteropsidinae*, *Lutrariinae*, *Zenatiinae*, and *? Anatinellinae*.

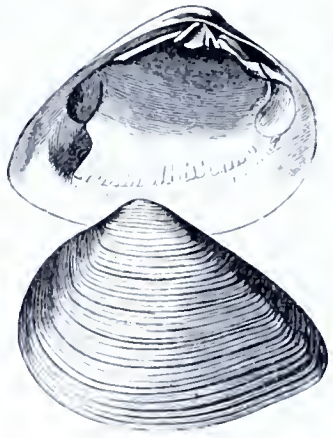


Fig. 775.

Mactra Podolica, Eichw. Miocene (Sarmatian Stage); Wiesen, near Vienna.

Mactra, Linn. (Fig. 775). Ligament and resilium separated by a shelly septum. Tertiary and Recent.

Sub-genera: *Mactra* s.s., *Coelomactra*, *Mactroderma*, *Mactrotoma*, Dall; *Mactrella*, Gray.

Spisula, Gray. Ligament and resilium not separated, the former more or less external. Cretaceous to Recent.

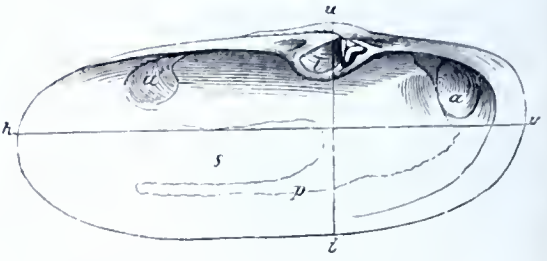


Fig. 776.

Lutraria elliptica, Roissy. Pliocene; Rhodes. 2/3.

Sub-genera: *Hemimactra*, Swains.; *Leptospisula*, Dall; *Cymbophora*, Gabb; *Schizodesma*, Gray.

Mulinia, Gray. Ligament and resilium immersed in the same socket. Miocene and Recent.

Rangia, Desm. (*Gnathodon*, Gray, non Goldfuss). Like *Mulinia*, but with elongated laterals, and the anterior lateral hooked at the umbonal end. Estuarine.

Pteropsis, Conrad. Eocene. *Labiosa* (Schmidt), Möller. Miocene and Recent.

Lutraria, Lam. (Fig. 776). Soleniform, hinge Mactroid. Tertiary and Recent.

Tresus, Gray (*Schizothaerus*, Conr.); *Eastonia*, Gray; *Heterocardia*, Desh. Tertiary and Recent. *Zenatia*, Gray; *Anatinella*, Sow. Recent.

[1] Cf. *Dall, W. H.*, Synopsis of a Review of the Genera of Recent and Tertiary Mactridae and Mesodesmatidae (Proc. Mal. Soc. vol. I. pp. 203-213), March 1895.

Family 39. **Cardiliidae.** Dall.

Shell cordiform, with prominent prosogyrous beaks, small, thin, radially sculptured; posterior adductor scar impressed upon a radial myophoric lamina, the anterior scar elongated, pallial line not sinuated; ligament external, seated on nymphs; resilium internal connecting projecting chondrophores; hinge without laterals, but the cardinal teeth as in Mactra. Tertiary to Recent.

Cardilia, Deshayes. Eocene and Recent.

Family 40. **Mesodesmatidae.** Deshayes.

Shell solid and heavy, usually Donaciform, with erect or opisthogyrate beaks, otherwise as in the Mactridae; siphons naked, not united. Tertiary to Recent.

Mesodesma, Desh. Tertiary and Recent. *Mactropsis*, Conr. Eocene. *Atactodea*, Dall (*Paphia*, Lam.; *Eryx*, Swains.); *Davila*, Gray; *Anapella*, Dall. Recent. *Ervilia*, Turton (Fig. 777). Tertiary and Recent. *Caecella*, Gray. Recent, fluviatile.

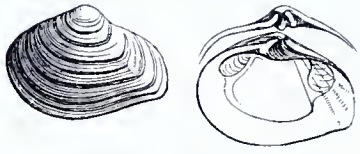


Fig. 777.

Ervilia Podolica, Eichw. Miocene (Sarmatian Stage); Wiesen, near Vienna. 1/1.

E. Asthenodonta.

Hinge often essentially Mactroid, but usually degenerate or obsolete, owing to modifications induced by the burrowing habit.

Superfamily 16. **MYACEA. Menke** (emend.)

Burrowing, long siphoned, frequently inequivalve Pelecypods, usually with the mantle lobes largely united below, more or less united siphons, and degenerate hinge apparatus.

Family 41. **Myacidae.** Woodward.

Shell substance cellulo-crystalline, earthy, with a conspicuous epidermis; valves unequal, more or less elongate, rounded in front and gaping behind; adductor scars subequal; pallial line sinuated; shell margins plain; area obsolete or none; ligament and resilium internal, opisthodetic, attached in the left valve to a projecting chondrophore merging with the dorsal margin behind, and in the right valve to an inconspicuous, usually subumbonal chondrophore; hinge edentulous; siphons united, with a horny tunic, not wholly retractile. Tertiary and Recent.

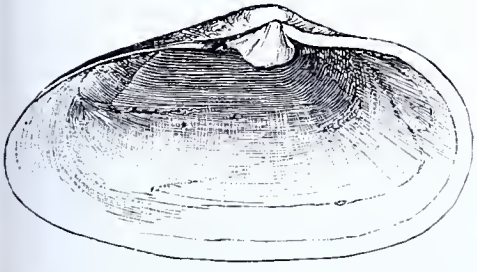


Fig. 778.

Mya arenaria, Lin. Pleistocene (Glacial Deposits); Bohuslän, Sweden.

Mya, Linn. (Fig. 778). Smooth externally. Tertiary and Recent.

Sub-genera: *Platyodon*, Conr. Surface decussated, siphon with horny appendages. *Cryptomya*, Conr. Small, the pallial line discrepant in the two valves. *Sphaenia*, Turton. Minute, byssiferous, nestling. *Tugonia*, Gray. Recent.

Family 42. **Corbulidae.** Fleming.

Shell small, much as in Mya, but the pallial line feeble or obsolete, the ligament usually sub-external, separated from the resilium, which is internal, alivincular, and

amphidetic; the chondrophore is received into a socket of the opposite valve, not merged with the valve margin; hinge with one or two sub-umbonal projecting teeth, and rarely obscure traces of laterals; the posterior gape inconspicuous; siphons short, united, naked, wholly retractile. Trias to Recent.

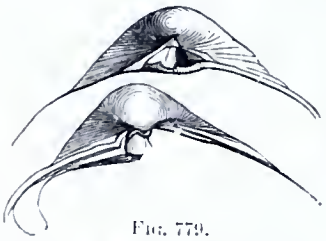


Fig. 779.

Corbula (*Bicorbula*) *gallica*, Lam. Calcaire Grossier; Damery, near Epernay, France. Hinge, 1/1.

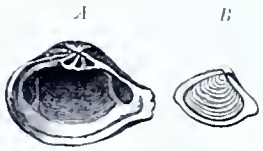


Fig. 780.

A, *Corbula carinata*, Duj. Miocene; Potzleinsdorf, near Vienna. *B*, *C. angustata*, Sow. Upper Cretaceous; Gosau.

Corbula, Lam. (Figs. 779, 780). Small, ovate, rostrate, very inequivalve, the right valve convex, larger, with a prominent tooth in front of the pit for the resilium, left valve with a flattened chondrophore, and usually a posterior tooth. Trias to Recent.

Sub-genera: *Erodona*, Daudin (*Azara*, d'Orb.; *Potamomya*, Sow.) Pallial sinus obsolete, fluviatile. Pleistocene and Recent. *Bothrocorbula*, Gabb. With a lunule deeply indented into the cavity of the valves. Tertiary and Recent. *Corbulamella*, Meek. With an anterior myophore. Cretaceous. *Anisothyris*, Conr. (*Pachydon*, Gabb). Pliocene. *Paramya*, Conr.; *Corbulomya*, Nyst. Tertiary and Recent.

Family 43. **Saxicavidae.** Gray.

Shell substance as in Mya; epidermis conspicuous; valves equal, free, rude, and often irregular, more or less elongated and gaping, not fully covering the animal; adductor scars often irregular, the pallial line discontinuous or irregular, the sinus distinct; shell margins smooth; area obsolete; ligament and resilium external, parivincular, seated on strong nymphs, sometimes widely extended; hinge without laterals, with few feeble or obsolete sub-umbonal cardinals. Cretaceous to Recent.

Saxicava, Fleuriau (*Glycimeris*, Schum.; *Hiatella*, Daudin; *Byssomya*, Cuvier; *Agina*, Turton). Hinge edentulous in the adult, with one or two cardinals in the young, boring in the softer rocks. Tertiary and Recent. Sub-genus *Panomya*, Gray (*Chaenopea*, Mayer).

Panopea, Menard (*Glycimeris*, Lam. 1799, non Da Costa), (Fig. 781). Large, gaping widely behind and slightly in front; surface concentrically, or feebly sculptured; an obscure tooth in each valve. Cretaceous to Recent.

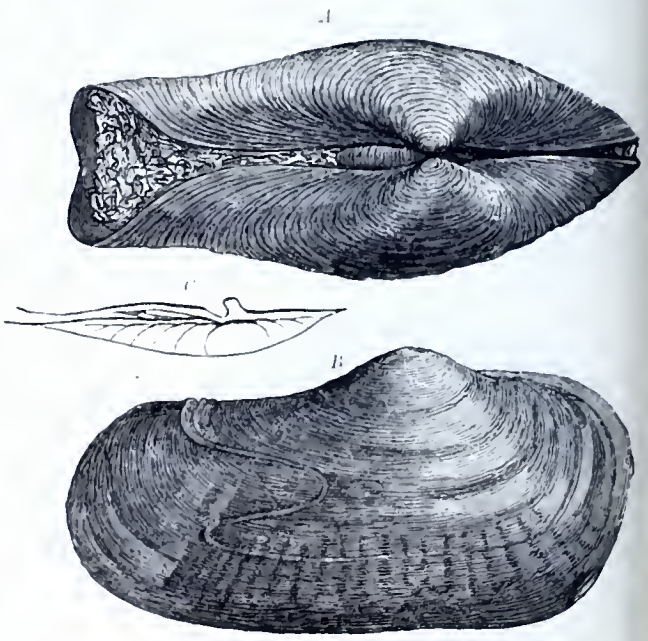


Fig. 781.

Panopea Menardi, Desh. Miocene; Vienna Basin. *A*, Dorsal view of valves. *B*, Internal cast. *C*, Hinge plate seen from above, 1/2.

Cyrtodaria, Daudin (*Glycimeris*, Lam. 1801). Solenoid with strong epidermis. Pliocene and Recent.

Family 44. **Gastrochaenidae.** Gray.

Shell substance as in Saxicava; valves equal, widely gaping in front; adductor scars unequal, the anterior smaller; pallial sinus deep, margins simple; area none; ligament and resilium external, parivincular; hinge with a single obsolete cardinal or wholly edentulous; animal frequently forming an external protective tube to supplement its burrow, but to which it is in no way attached. ? Permian. Trias to Recent.

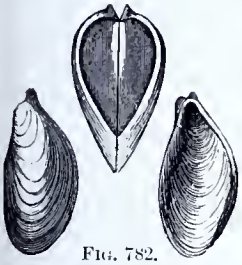


Fig. 782.

Gastrochaena angusta, Desh. Eocene (Sables moyens); Valmandois, near Paris.

Fig. 783.

Gastrochaena Deslongchampsii, Laube. Middle Jura; Balin, near Cracow. Cast of burrow including one of the valves, 1/1.

This group stands between the *Myacea* and *Adesmacea*, verging on the latter. Many of its characters are adaptive, and are repeated in the *Ensiphonacea*, but morphologically its relations to the *Saxicavidae* seem close.

Gastrochaena, Spengler (*Chaena*, Retz.; *Rocellaria*, Blainv.), (Figs. 782, 783). Bores cylindrical or pear-shaped cavities in rock, shell, or coral. Trias to Recent.

Fistulana, Brug. Secretes calcareous tubes which stand upright in the sand or mud.

Superfamily 17. ADESMACEA. Blainville.

Gills with direct and reflected laminae, long, united, extended into the branchial siphon; posterior adductor usually in front of the visceral ganglion, anterior adductor external to the cavity of the valves, exerted in a contrary sense to the posterior muscle; hinge margin reflected, edentulous; ligament obsolete; a myophoric process extending freely into the valve from the sub-umbonal cavity.

Family 45. **Pholadidae.** Fischer.

Shell cellulo-crystalline, with a thin epidermis; valves more or less gaping in front and behind, with inconspicuous beaks and reticulate, often spinose sculpture; in the adult supplemented by accessory shelly pieces, always attached to the valves, but not by an exterior shelly tube like that of the Gastrochaenidae: the antero-dorsal margins more or less extensively reflected, the postero-ventral approximated; pallial line sinuated, area none: ligament and resilium usually absent, an obsolete remnant of the resilium and chondrophore sometimes present in the left valve. ? Carboniferous, Jura to Recent.

Pholas, Linn. (Fig. 784). Surface divided by grooves into areas which often have diverse sculpture; the adult often provided with accessory shelly plates, each of which

Fig. 784.

Pholas Levesquei, Watelet. Eocene; Cuise de la Mothe.

when seated in front of the beaks has been named a "protoplax," when above the beaks, "mesoplax," when behind the beaks between the valves "metaplax," and when between the valves ventrally (*Martesia*), "hypoplax." A calcareous septum, secreted after the completion of the burrow, and occupying the pedal gape of the valves, is called the "callum." The addition of these plates and appendages during growth so

changes the appearance of the shell that old and young stages have frequently been described as specifically or even generically distinct. Typical Pholads date from the Jura. Many subgenera have been named.

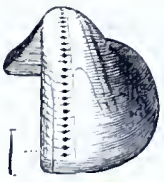


Fig. 785.

Turnus (*Xylophagella*) *elegantulus*, Meek. Upper Cretaceous; Idaho. Enlarged (after Meek).

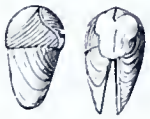


Fig. 786.

Martesia conoidea, Desh. Eocene; Anvers, near Paris. 1/1.

Turnus, Gabb (Fig. 785). Cretaceous. *Martesia*, Leach (Fig. 786). Carboniferous to Recent. *Jouannetia*, Desm. Tertiary and Recent. *Teredina*, Lam. Valves in the adult stage soldered together and to a thick adventive calcareous tube. Eocene.

Family 46. **Teredinidae**. Scacchi.

Shell much reduced, equivalve, auriculate, widely gaping, the valves opposited ventrally only on the surface of a parietal tubercle; adductor scars unequal, the anterior marginal very small: pallial line coincident with the valve margins: a styloid myophore projecting from the cavity of the beaks: mantle secreting a calcareous lining to the burrow; pallets variable in form, the valves without attached accessory shelly plates: area none: hinge margin reflected, edentulous: ligament absent or obsolete: anterior adductor degenerate, attached on the anterior edges of the valves, and covered only by the mantle: animal boring, chiefly in wood. Carboniferous (?), Jura to Recent.

Fig. 787.

A, Valves of the recent *Teredo Norvegica*, Spengl; inner and outer views. *B*, Pallet of *Xylotrya* sp. *C*, Pallet of *Teredo* sp. *D*, Casts of borings of *Teredo Tournali*, Leym. Eocene; Kressenberg, Bavaria.

Teredo, Linn. (Fig. 787, *A*, *C*). Pallets simple, spatuliform. Jura to Recent.

Xylotrya, Leach (Fig. 787, *B*). Pallets articulated, bipinnate. Tertiary and Recent.

The name *Teredolites*, Leymerie, has been proposed for the casts of borings of fossil Teredos (Fig. 787, *D*). The problematical genus *Polorthus*, Gabb, from the American Cretaceous, has been referred to this family. The Palaeozoic species are known only by burrows, which are of somewhat doubtful origin.

Vertical Range of the Pelecypoda.

Pelecypods make their appearance as extreme rarities in the Lower Cambrian,[1] being represented only by the doubtful *Fordilla* and the tiny *Modioloides*. Even in the Ordovician they are still rare. *Modiolopsis*, *Ctenodonta*, *Palaearca*, *Eopteria*, and *Glyptarca* have been sparingly found. In the Silurian a considerable augmentation of the number of bivalves is observable, as many as eighty species having been distinguished in the fauna of the small island of Gottland alone.

A very marked difference in geological range is perceptible among the three orders into which the class is divided. The *Prionodesmacea*, including most of Neumayr's *Palaeoconcha*, are pre-eminently characteristic of the Palaeozoic faunas. Of the forty-two families referred to this order, no less than nineteen occur in the Silurian, to which seven are added during the Devonian, only three in the Carboniferous, and one in the Permian. From these ancient stocks only seven Prionodesmacean families are evolved during the whole of the Mesozoic, and but two in the Tertiary, while three are Recent. Omitting offshoots, but four families cover the whole range of geologic time from

[1] Cf. *Walcott, C. D.*, Fauna of the Olenellus Zone (10th Ann. Rep. U. S. Geol. Surv., 1890).

the Silurian, and of these the recent representatives are everywhere recognised as constituting the most distinctively archaic type of Pelecypod structure now existing.

The order *Anomalodesmacea* is represented in the Palaeozoic solely by its radical, the *Pholadellidae:* eight of its sixteen families originate in the Mesozoic and Tertiary, and, with the exception of the *Pholadellidae* and *Pleuromyacidae*, all have endured until the present time. Only one family appears to be exclusively Recent.

The *Teleodesmacea* are distinctively modern, although foreshadowed in the Palaeozoic by Cypricardian, Lucinoid, and Allodesmid radicals (the Solenoid radical is still questionable). Of forty-seven families thirty can be first definitely recognised in the Mesozoic, twelve originate in the Tertiary, two are exclusively recent, and only a single one can be traced continuously from the Palaeozoic to the recent fauna.

Of the Prionodesmacean families, 10·5 per cent survive; of the Teleodesmacean 71 per cent; and of the Anomalodesmacean 88 per cent. If it were not for the mortality among the *Chamacea* and *Rudistae*, the ratio of survival among the Teleodesmacean families would be 95 per cent. Of 105 families which have been discriminated during the whole history of the class 76, or about 72·3 per cent, are represented in the existing fauna. Families have originated in the various geological epochs as follows:— Cambrian 1, Silurian (Murchisonian) 20, Devonian 10, Carboniferous 3, Permian 2, Trias 13, Jura 14, Cretaceous 18, Eocene 15, Miocene and Pliocene 3, Pleistocene and Recent 6. From this it appears that the development of the group, judged by the increase of families, was most intense during the Silurian, thereafter rapidly decreasing until the Trias, then gradually increasing until the Cretaceous, after which the rate of differentiation again rapidly declined. It is noted that in the Palaeozoic the Pelecypods form about one-quarter of all the mollusks known from this era; in the Jura and Cretaceous about one-half, and in the Tertiary about one-third of this number.

The Silurian is especially characterised by the presence of Taxodont, Palaeoconch, and the older forms of Schizodont Pelecypods. The *Vlastidae, Cardiolidae, Antipleuridae, Ctenodontidae, Pterineidae, Ambonychiidae*, and *Modiolopsidae* are shared with the Devonian.

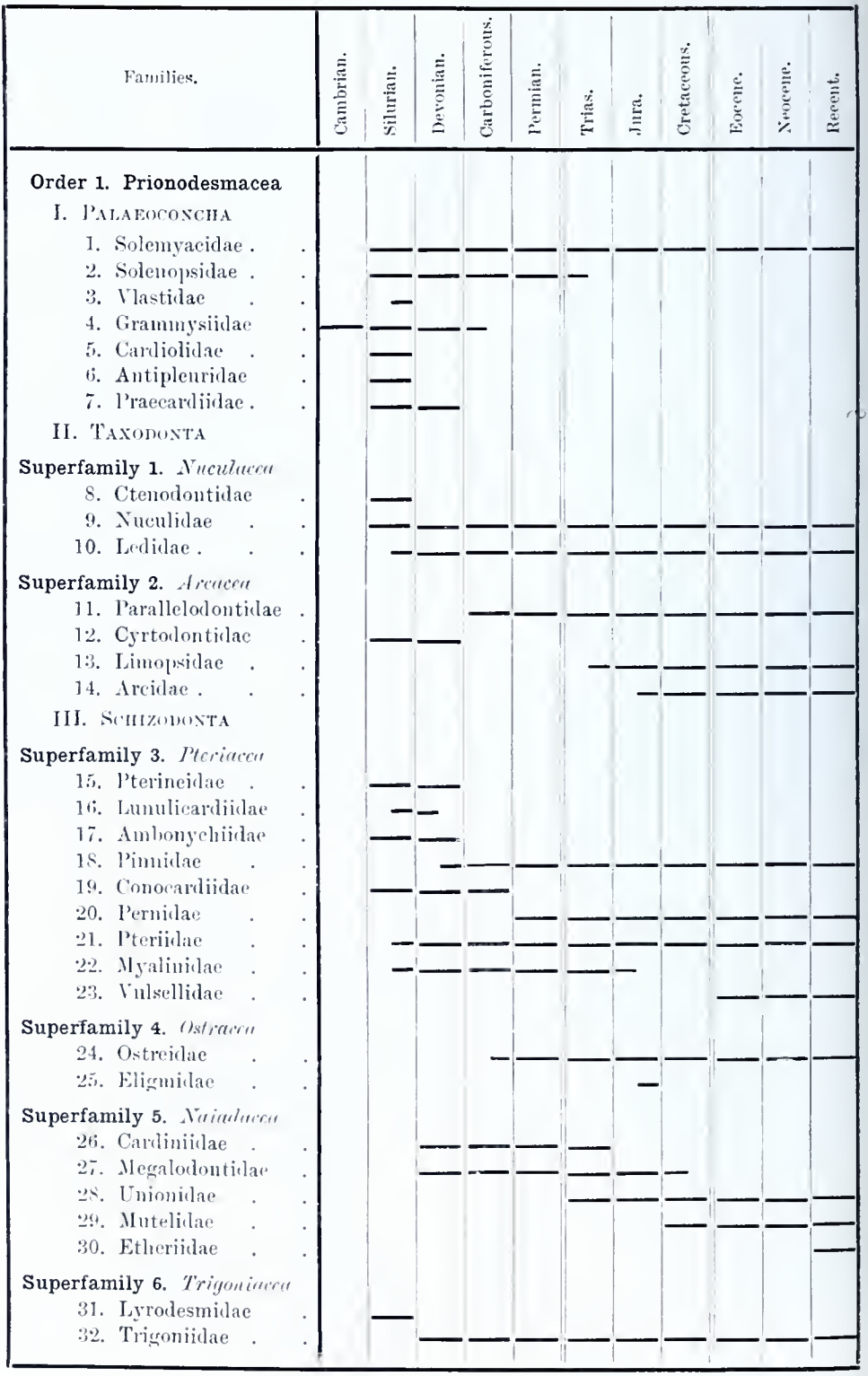
The Devonian has no families solely characteristic, but the brackish water *Cardiniidae*, the *Megalodontidae, Trigoniidae, Pinnidae, Pectinidae*, and *Mytilidae* first take rise in this period, and the sinupalliate *Allorisma* is the first Pelecypod showing clear evidence of retractile siphons.

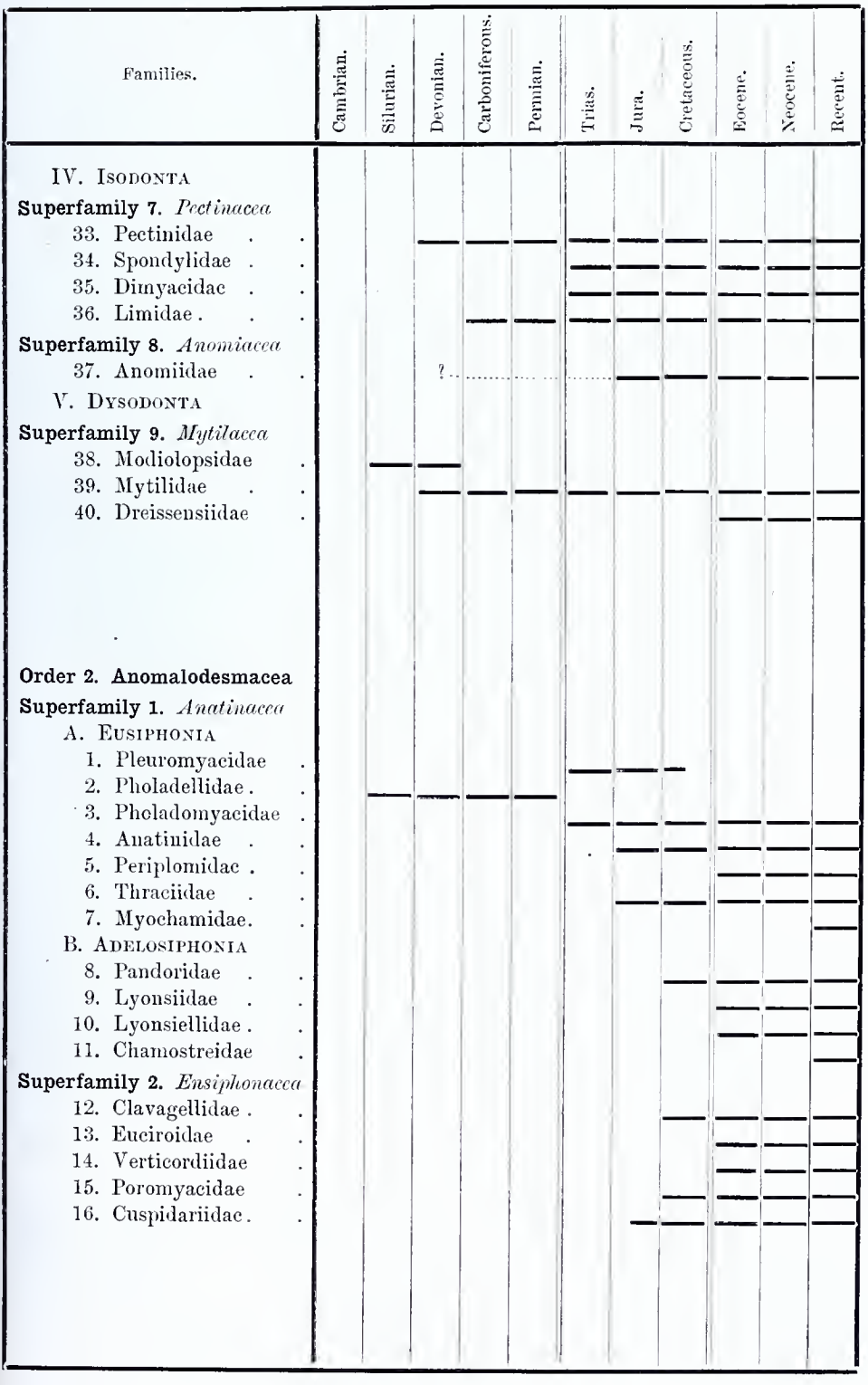
The Carboniferous is marked by the appearance of *Parallelodon* and its allies, the *Limidae* and *Ostreidae*, and some precursors of the *Lucinacea* and *Pholadacea*. The *Pernidae* and *Gastrochaenidae* make their advent in the Permian; but, on the whole, the Carbonic fauna persists throughout this period. In the Trias, however, important changes take place; many old genera disappear, and such forms as *Limopsidae*, the true *Uniones*, *Spondylus*, *Dimya*, the *Pleuromyacidae*, *Pholadomyacidae*, *Astartidae*, *Lucinacea*, *Cardiidae*, and *Corbulidae* enter upon the scene.

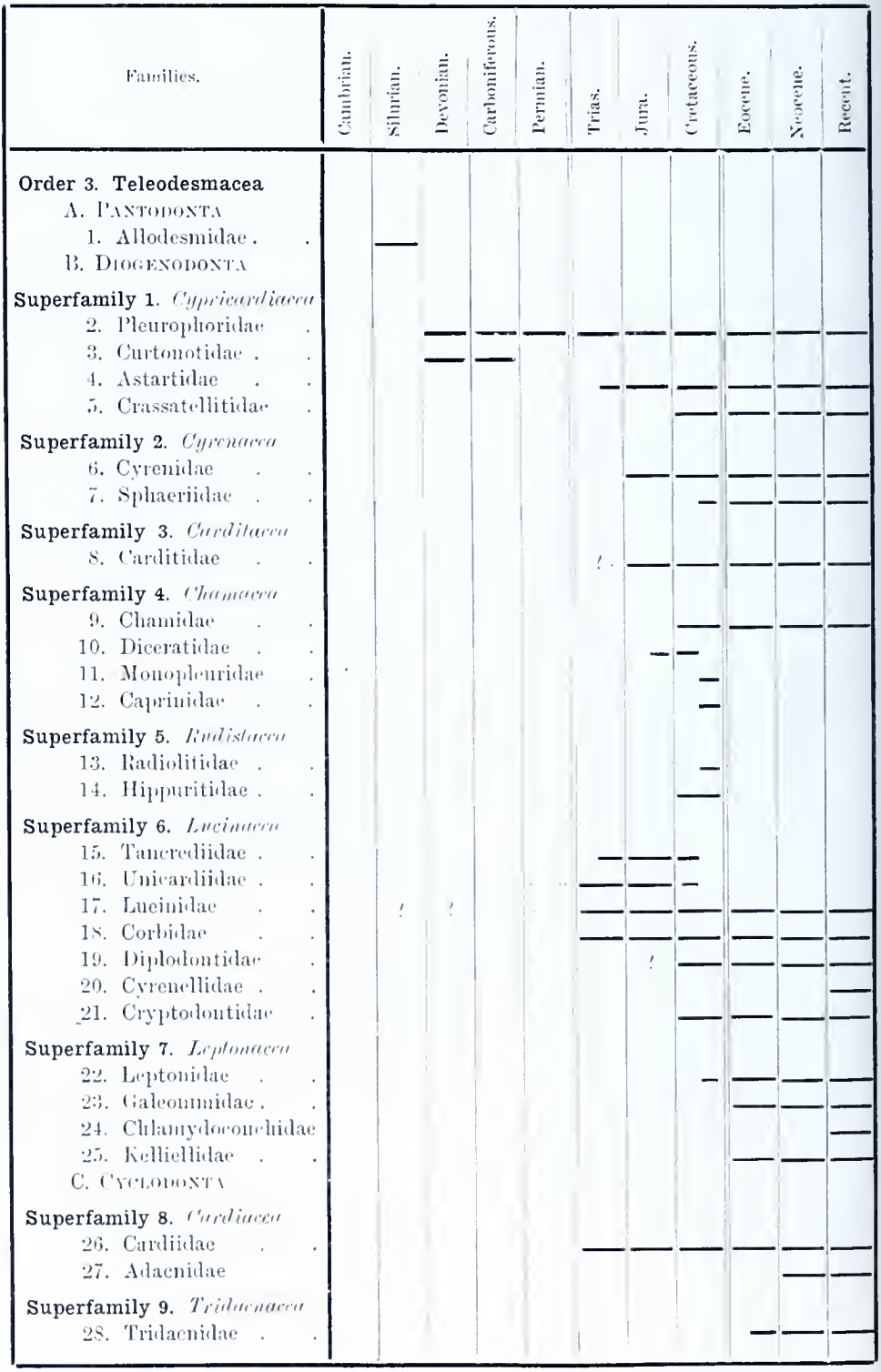
During the Jura, genuine *Arcidae*, *Anomia*, *Eligmus*, various *Anatinacea*, *Cyrena*, *Diceras*, *Isocardia*, and the Teleodont *Veneridae*, *Tellinidae*, *Donacidae*, and *Pholadacea* are initiated. The character of the Cretaceous is strongly influenced by the aberrant and short-lived *Chamacea* and Rudistids. The *Mutelidae*, *Pandoridae*, *Clavagellidae*, *Poromyacidae*, *Crassatellitidae*, *Cryptodontidae*, *Petricolidae*, true Solens, the *Mactridae*, and *Saxicavidae*, also take their origin during this period.

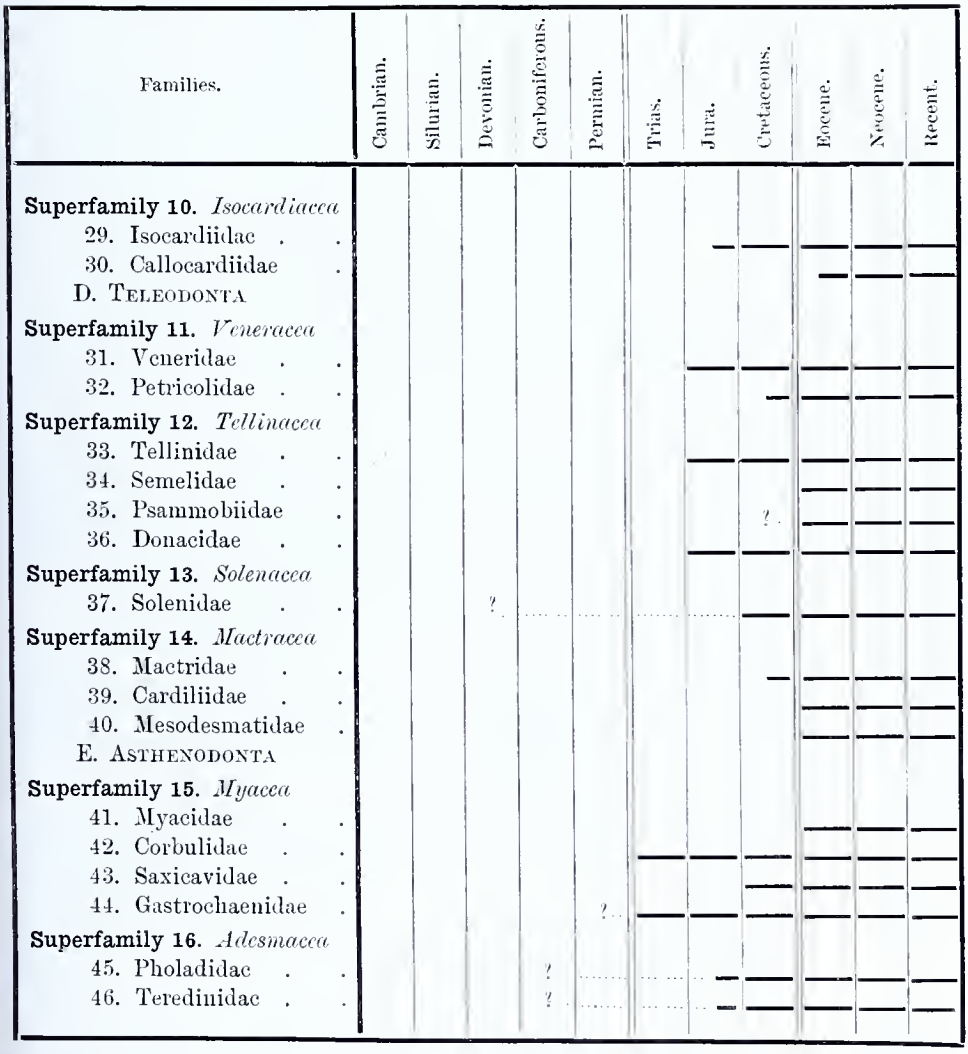
With the beginning of the Tertiary a gradual approximation to present conditions takes place. The *Rudistae* have disappeared, the Dysodonts are on the decline, and the Teleodesmacean types on the increase. Numerous *Anatinacea*, *Leptonacea*, *Tridacnidae*, *Callocardiidae*, *Semelidae*, *Mesodesmatidae*, and *Myacidae* appear. At the close of the Eocene, the wide distribution of many types now characteristic of warm, temperate, or tropical waters begins to be restricted; and during the Miocene the faunal boundaries of mollusks depending upon temperature conditions are laid down nearly on existing lines.

The following table indicates more exactly the geological range of the families of Pelecypods according to our present information:—


Families.
Cambrian.
Silurian.
Devonian.
Carboniferous.
Permian.
Trias.
Jura.
Cretaceous.
Eocene.
Neocene.
Recent.
Order 1. Prionodesmacea
I. Palaeoconcha
1. Solemyacidae
2. Solenopsidae
3. Vlastidae
4. Grammysiidae
5. Cardiolidae
6. Antipleuridae
7. Praecardiidae
II. Taxodonta
Superfamily 1. Nuculacea
8. Ctenodontidae
9. Nuculidae
10. Ledidae
Superfamily 2. Arcacea
11. Parallelodontidae
12. Cyrtodontidae
13. Limopsidae
14. Arcidae
III. Schizodonta
Superfamily 3. Pteriacea
15. Pterineidae
16. Lunulicardiidae
17. Ambonychiidae
18. Pinnidae
19. Conocardiidae
20. Pernidae
21. Pteriidae
22. Myalinidae
23. Vulsellidae
Superfamily 4. Ostracea
24. Ostreidae
25. Eligmidae
Superfamily 5. Naiadacea
26. Cardiniidae
27. Megalodontidae
28. Unionidae
29. Mutelidae
30. Etheriidae
Superfamily 6. Trigoniacea
31. Lyrodesmidae
32. Trigoniidae


Families.
Cambrian.
Silurian.
Devonian.
Carboniferous.
Permian.
Trias.
Jura.
Cretaceous.
Eocene.
Neocene.
Recent.
IV. Isodonta
Superfamily 7. Pectinacea
33. Pectinidae
34. Spondylidae
35. Dimyacidae
36. Limidae
Superfamily 8. Anomiacea
37. Anomiidae
?
V. Dysodonta
Superfamily 9. Mytilacea
38. Modiolopsidae
39. Mytilidae
40. Dreissensiidae
Order 2. Anomalodesmacea
Superfamily 1. Anatinacea
A. Eusiphonia
1. Pleuromyacidae
2. Pholadellidae
3. Pholadomyacidae
4. Anatinidae
5. Periplomidae
6. Thraciidae
7. Myochamidae
B. Adelosiphonia
8. Pandoridae
9. Lyonsiidae
10. Lyonsiellidae
11. Chamostreidae
Superfamily 2. Ensiphonacea
12. Clavagellidae
13. Euciroidae
14. Verticordiidae
15. Poromyacidae
16. Cuspidariidae


Families.
Cambrian.
Silurian.
Devonian.
Carboniferous.
Permian.
Trias.
Jura.
Cretaceous.
Eocene.
Neocene.
Recent.
Order 3. Teleodesmacea
A. Pantodonta
1. Allodesmidae
B. Diogenodonta
Superfamily 1. Cypricardiacea
2. Pleurophoridae
3. Curtonotidae
4. Astartidae
5. Crassatellitidae
Superfamily 2. Cyrenacea
6. Cyrenidae
7. Sphaeriidae
Superfamily 3. Carditacea
8. Carditidae
Superfamily 4. Chamacea
9. Chamidae
10. Diceratidae
11. Monopleuridae
12. Caprinidae
Superfamily 5. Rudistacea
13. Radiolitidae
14. Hippuritidae
Superfamily 6. Lucinacea
15. Tancrediidae
16. Unicardiidae
17. Lucinidae
18. Corbidae
19. Diplodontidae
20. Cyrenellidae
21. Cryptodontidae
Superfamily 7. Leptonacea
22. Leptonidae
23. Galeommidae
24. Chlamydoconchidae
25. Kelliellidae
C. Cyclodonta
Superfamily 8. Cardiacea
26. Cardiidae
27. Adacnidae
Superfamily 9. Tridacnacea
28. Tridacnidae



[Grateful acknowledgments are due to Dr. W. H. Dall, of the United States National Museum, for having revised and in large part rewritten the preceding chapter on the Pelecypods. It is to be regretted, however, that limits of space necessitated a partial abbreviation of the original text, for which the Editor alone is responsible.—Trans.]

Class 2. SCAPHOPODA. Bronn.[1]

(*Cirrhobranchiata*, Blainville; *Solenoconchia*, Lacaze-Duthiers; *Prosopocephala*, Stoliczka.)

Aquatic, marine, bilaterally symmetrical Mollusks, protected by an external, tubular, somewhat curved and tapering shell, open at both ends, the concave side of which is dorsal; the shell secreted by a mantle of the same shape, the larger, anterior opening of which is provided with a circular muscular thickening, the smaller opening serving as outlet for organic waste and genital products. Mouth furnished with a radula, borne on a cylindrical snout, and surrounded by a rosette of leaf-like appendages; a cluster of numerous exsertile filaments (captacula) springing from its base. Otocysts present, but no eyes or tentacles. Foot rather long, conical, with lateral lobes, and adjacent to the snout ventrally.

Gills are wanting, the general surface assuming respiratory functions. Liver large, bilateral; intestine strongly folded, the anus ventral and rather anterior, and kidney orifices adjacent to it. Heart rudimentary, with a single chamber. Nervous system with well-developed ganglia united by commissures. Reproduction without copulation, the sexual products voided through the right kidney.

Scaphopods are without exception marine, and for the most part inhabit deep water. There are no littoral species. They live embedded in mud or sand, with only the smaller end of the shell projecting above the surface. Their food consists chiefly of Foraminifera and similar organisms, captured by the filamentary *captacula*.

The tubular, curved shell, open at both ends, is characteristic of the class, the tubular shells of certain Gastropods and Cephalopods being invariably closed at the smaller end. Some tubicolous Worms (*Serpulidae*) form a similar shell, but it is composed of two layers only, instead of three as in Scaphopods, the growth is more irregular, and its microscopic structure very different.

Fig. 788.

Pyrgopolon Mosae, Montf. Upper Cretaceous; Belgium.

The shell of Scaphopods increases by successive increments at the larger end, and at the same time loses by wear and absorption at the smaller end. The posterior slits or notches occurring in some species are therefore formed by reabsorption of the previously solid shell wall, and have a genesis wholly different from the slits or fissures of *Pleurotomaria*, *Fissurella*, and other Gastropods.

Various genera described as Scaphopods have since been found to belong to the *Serpulidae*. Such are *Pyrgopolon*, Montf. (Fig. 788), from the Maestricht of Belgium, also known as *Entalium*, Defr., and *Pharetrium*, König; and *Hanulus*, Morton (*Falcula*, Conrad), of the American Cretaceous. The Cambrian genus *Spirodentalium*, Walcott, in which the shell has spiral striae, is at present too

[1] Literature (see also, under the head of Mollusca, pp. 344, 345):

Deshayes, G. P., Anatomie et Monographie du Genre Dentale (Mém. Soc. Hist. Nat., Paris, vol. II. pp. 321-378), 1825.

Lacaze-Duthiers, H. de, Histoire de l'organisation et du développment du Dentale (Ann. des Sci. Nat. [4]. vols. VI.-VIII.), 1856-57.

imperfectly known to justify its reference to the Scaphopods, or even to the Mollusca.

Family 1. **Dentaliidae.** Gray.

Scaphopoda having a conic foot with an encircling sheath expanded laterally and interrupted dorsally. Shell tubular, curved, regularly tapering throughout, not contracted anteriorly, sculptured or smooth. Ordovician to Recent.

Dentalium, Linn. (Figs. 789, 790). Characters those of the family. Beginning with a few species in the Ordovician, the number increases slowly until the Cretaceous. A great acceleration then ensues, which continues to the present. About 275 fossil and 150 recent species known. Various authors have attempted to subdivide the genus upon characters of the posterior slit of the shell, but this has proved to vary widely even among individuals. The following sub-genera based upon the system of sculpture and shape of the tube appear more stable :—

Fig. 789.

Dentalium sexangulare, Lam. Pliocene; Asti, Italy.

Dentalium, s. str. (Fig. 789). Shell with strong longitudinal ribs, apical notch short or wanting. Eocene to Recent.

Antalis, Adams (*Entalis*, Gray non Sowb.: *Entaliopsis*, Newton and Harris), (Fig. 790, *A*). Shell with longitudinal riblets or striae at least in the young; apex with a short ventral slit and a sheath. Cretaceous to Recent.

Heteroschisma, Simr. With longitudinal riblets and a dorsal slit. Recent.

Fissidentalium, Fischer. Large and solid, with many longitudinal ribs or striae; a long ventral slit usually present. Eocene to Recent. *Schizodentalium*, Sowb., in which the slit is interrupted into a series of holes, is probably a modification of this group.

Graptacme, Pils. and Sharp. Surface with close, fine longitudinal striae near apex only, or throughout. Tertiary and Recent.

Laevidentalium, Cossm. Arcuate, smooth, with growth-lines only, circular in section, apex simple or notched. Silurian ? to Recent.

Rhabdus, Pils. and Sharp. Smooth, glossy, nearly straight, sub-circular in section, apex entire. Recent.

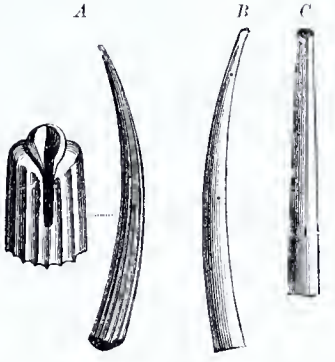


Fig. 790.

A, D. (*Antalis*) *Kickxi*, Nyst. Oligocene; Weinheim, near Alzey. *B, D.* (*Fustiaria*) *lucida*, Desh. Eocene; Cuise la Mothe. 1/1. *C*, Posterior portion of same enlarged, showing slit.

Episiphon, Pils. and Sharp. Small and very slender, smooth, the apex generally with an inserted tube. Oligocene to Recent.

Compressidens, Pils. and Sharp. Small, much tapering, vertically compressed, smooth. Eocene to Recent.

Lobantale, Cossm. Shell compressed, with two internal longitudinal ribs. Eocene.

Fustiaria, Stol. (Figs. 790, *B, C*). Shell with a very long and linear ventral cleft posteriorly. Cretaceous to Recent.

Sars, M., Om Siphonodentalium vitreum, en ny Slaegt af Dentalidernes Familie. Universitets-Program, Christiana, 1861.

Stoliczka, F., Palaeontologia Indica. Cretaceous Fauna of Southern India, vol. II., 1867-68.

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Simroth, H., Mollusca in Bronn's Classen und Ordnungen des Thierreichs, vol. III. pp. 356-467, 1893-95.

Plagioglypta, Pils. and Sharp. Surface with extremely oblique, sinuous, encircling striae (*D. undulatum*, Münst.) Carboniferous to Trias.

Family 2. **Siphonodentaliidae.** Simroth.

Scaphopoda having the foot either expanded distally in a symmetrical disk with crenate continuous edge, or simple and vermiform, without developed lateral processes. Shell small and generally smooth, often contracted towards the mouth. Cretaceous to Recent.

Although this family is usually characterised by a small smooth shell, the essential difference from the *Dentaliidae* is in the form of the foot. Typical forms of *Cadulus* appear in the Cretaceous; the remaining genera are Tertiary and Recent.

FIG. 791.

A, *Cadulus* (*Polyschides*) *denticulatus*, Desh. Calcaire Grossier; Damery, near Epernay. *B*, *Cadulus* (*Dischides*) *bifissuratus*, Desh. Calcaire Grossier; Grignon, near Paris. *C*, *Cadulus ovulum*, Phil. Tortonian; Monte Gibbio. *D*, *Cadulus olivi*, Scac. Tortonian; Monte Gibbio, near Sassuolo, Italy.

Entalina, Monts. Shell *Dentalium*-like, largest at the aperture, thence tapering to the apex; strongly ribbed, and angular in section near the apex. Miocene to Recent.

Siphonodentalium, Sars (*Pulsellum*, Stol.; *Siphonentalis*, Sars). Shell an arcuate, slightly tapering tube, circular in section or nearly so, and smooth externally. Apex rather large, typically slit into lobes, but sometimes simple. Pliocene to Recent.

Cadulus, Phil. (*Gadus*, Desh.; *Gadila*, Gray; *Helonyx*, Stimp.), (Figs. 791, *C*, *D*). Shell tubular, circular or oval in section, swollen near the middle, or anteriorly, contracting toward the apertnre. Cretaceous to Recent.

Typical forms with simple anal orifice appear first in the Cretaceous, *Dischides*, Jeffr. (Fig. 791, *B*), with two lateral slits, and *Polyschides*, Pils. (Fig. 791, *A*), with several notches appear in the Eocene. All continue to the present.

Class 3. AMPHINEURA. Ihering.[1]

Aquatic, marine, bilaterally symmetrical Mollusks, with the head partially or not differentiated; in form worm-like with a ventral groove or none, or oval, flattened, with a foot adapted for creeping. Nervous system consisting of an oesophageal ring with ganglia and four longitudinal cords, two ventral and two lateral; no cephalic eyes, tentacles, or otocysts. Gills paired or many, posterior or lateral; mouth anterior, usually with a radula; anus posterior, median. External surface with a series of shelly plates, or stiffened with calcareous spicules.

[1] Literature:

Ihering, H. v., Vergleichende Anatomie des Nervensystems und Phylogenie der Mollusken, 1877.
Dall, W. H., On the Genera of Chitons (Proc. N. S. Nat. Museum, vol. IV. p. 279), 1881.
Hubrecht, A. A. W., A Contribution to the Morphology of the Amphineura (Quar. Journ. Microscop. Soc., vol. XXII. pp. 212-227), 1882. [Bibliography, pp. 226. 227.]
Rochebrune, A. T. de, Monographie des espèces fossiles appartenant à la classe des Polyplaxiphores (Ann. Sci. Geol., vol. XIV. pp. 1-74), 1883.
Pruvot, G., Sur l'organisation de quelques Néoméniéns des Côtes de France (Arch. Zool. Expér. et Génér. [2], vol. IX. pp. 699-805, 1891. [Bibliography, pp. 702, 703.]
Pilsbry, H. A., Monograph of the Polyplacophora. In Tryon and Pilsbry's Manual of Conchology, vols. XIV. and XV., 1892-93.

Order 1. APLACOPHORA.

Body vermiform with a ventral groove, the skin elsewhere beset with calcareous spicules; no dorsal shelly plates in the adult.

This is a degenerate group, represented in the recent fauna by about a dozen genera belonging to two families—*Chaetodermatidae* and *Neomeniidae*. Fossil remains are unknown.

Order 2. POLYPLACOPHORA. Blainville. Chitons.

Amphineura protected by a dorsal series of eight shelly valves and an encircling girdle; with differentiated head, and a ventral sole or foot adapted to creeping; gills numerous, occupying the groove between foot and girdle; radula present, heterodont; sexes separate.

The external covering in the *Polyplacophora*, or Chitons, consists of eight valves bound together by an encircling flexible band called the girdle. The anterior or head-plate (Fig. 792, *A*, below) is invariably semicircular, with the apex or *mucro* at the middle of the straight margin; the six succeeding plates are generally square (Fig. 793, below), with the apex posterior on the median line; and the posterior or tail-valve (Fig. 792, *B*) is semicircular or subcircular, with apex varying in position from in front of the middle to the hind margin. All of the plates are composed of two layers—an outer porous layer, the *tegmentum*, and an inner porcellanous one, the *articulamentum*. In most of the lower Chitons these layers are coextensive and have smooth edges; but in the higher forms the articulamentum projects beyond the outer layer into the substance of the girdle, in which it is firmly inserted. These projections at the outer or peripheral margin are termed *insertion plates*. They are generally slit or notched into so-called "teeth," which may be either smooth and sharp along the edge, or crenulated (*pectinated*). Insertion plates serve the function of binding the valves firmly to the girdle.

The anterior margin of each valve except the first one invariably shows two projections of the articulamentum called *sutural laminae* (Figs. 792, *B*, 793), which pass under the rear margin of the next anterior valve, thus preventing vertical displacement of the series. The tegumentum is traversed by a multitude of fine canals which terminate at the surface in minute sense organs. The position of the latter in dry or fossil valves is visible as a fine quincuncial punctation. In the highest Chitons a certain number of these sense organs have become enlarged and modified into eyes, easily recognised as pigmented dots in recent, and small pits in fossil specimens.

Polyplacophora make their appearance as early as the Ordovician; they are rare in the Silurian and Devonian, but somewhat more abundant in the Carboniferous. None of the Palaeozoic genera (*Eoplacophora*) are known to continue into the Mesozoic, but are replaced by types more related to modern Chitons (*Mesoplacophora*). Members of the most specialised sub-order, *Teleoplacophora*, are first encountered in the Eocene, although they doubtless arose earlier. About twenty Palaeozoic, five or six Mesozoic, and fifty Tertiary species have been described. Recent forms number several hundreds. A good many species supposed to be Chitons have been based upon barnacle

valves, fish scales, and other fragments. The recently described *Duslia insignis*, Jahn, is apparently a Crustacean; certainly not a member of the *Polyplacophora*.

Three sub-orders are recognised, according as the insertion plates are absent, or if present, unslit (*Eoplacophora*); developed, smooth, and slit into teeth (*Mesoplacophora*); or both slit and pectinated (*Teleoplacophora*).

Sub-Order A. EOPLACOPHORA. Pilsbry.

Polyplacophora with the tegumentum coextensive with the articulamentum, or with the latter projecting in smooth, unslit insertion plates; gills posterior.

Family 1. Gryphochitonidae. Pilsbry.

Insertion plates absent, sutural laminae small; one or both end-valves with the terminal margins elevated; form elongated and narrow. Palaeozoic.

Helminthochiton, Salter. Valves thin, mucro sub-central, low; end-valves not elevated terminally. Silurian.

Priscochiton, Billings. Similar in the non-sinuous head-valve, but beaks of the valves greatly produced backwards. Ordovician.

Gryphochiton, Gray (Fig. 792). Elongated, with small beaks and very small sutural laminae; terminal margins of end-valves strongly elevated; tail-valve with low, decurved mucro behind the middle. Carboniferous.

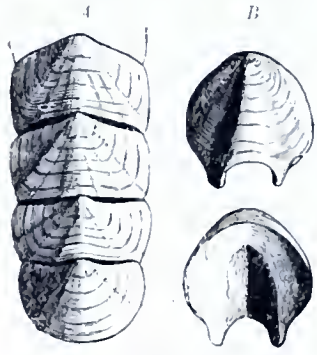

Fig. 792.

Gryphochiton priscus, Münst. Carboniferous; Tournay, Belgium. *A*, Anterior and three intermediate valves. *B*, Posterior valve, ventral and dorsal aspects. 1/1.

Pterochiton, Cpr. (*Anthraeochiton*, Rochebr.). Elongated, the valves strongly beaked and laterally excavated; tail-valve with depressed post-median mucro and no posterior sinus, anterior valve with the front margin elevated, sutural laminae large. Carboniferous.

Cymatochiton, Dall (*Protalochiton*, Rochebr.). Oval, elevated and granular, the valves short and wide, with small, low sutural laminae and distinct lateral areas; mucro of posterior valve post-median, elevated. Permian.

Probolaeum, Cpr. Elongated, elevated; valves very strongly beaked, the pleura projecting beyond the jugal tract; anterior valve sinuate in front, posterior valve unknown. Devonian.

Choneehiton, Cpr. Median valves as in *Gryphochiton*; posterior valve with the mucro thrown backward, as in *Cryptoplax*. Carboniferous.

Loricites, Cpr. Somewhat like the recent *Lorica*, but without insertion plates. Carboniferous.

Fig. 793.

Lepidopleurus virgifer, Sandb. Miocene; Waldböckelheim, near Creuznach, Germany. A median and a posterior valve. 2/1.

Family 2. Lepidopleuridae. Pilsbry.

Insertion plates absent, or present and unslit; end-valves with the terminal margins never elevated; form oval or oblong. Tertiary and Recent.

Lepidopleurus, Risso (*Leptochiton*, Gray), (Fig. 793). Small, oval; insertion plates entirely absent, sutural laminae small; girdle minutely scaly or chaffy. Eocene to Recent.

Hanleya, Gray. Like the last, except that the anterior valve has an unslit insertion plate, and the girdle is spiculose. Champlain to Recent.

Hemiarthrum, Cpr. Both anterior and posterior valves with smooth unslit insertion plates, the others lacking them; girdle downy, with small sutural pores. Recent.

Choriplax, Pils. Valves partly immersed in the minutely granulose girdle, all with thin, smooth insertion plates. Recent.

Sub-Order B. MESOPLACOPHORA. Pilsbry.

Insertion plates developed, slit, not vertically grooved or pectinated outside.

Family 1. Ischnochitonidae. Pilsbry.

Valves having the inner layer well covered by the outer. Surface of intermediate valves divided into lateral and central areas by a diagonal rib (often indistinct), extending from the beak to each anterior outer angle of tegumentum; or when this is not clearly the case, the posterior valve has a crescentic series of well-developed teeth; all valves with slits. Eocene to Recent.

Two sub-divisions of this family are recognised, according as the anterior and side slits correspond in position with ribs on the external surface or not. Among the genera included under the first head (*Callistoplacinae*) may be mentioned the following:—*Callistochiton*, *Nuttallina*, and *Callistoplax*, Carpenter; *Craspedochiton*, Shuttleworth; and *Ceratozona*, Dall. Representatives of the second sub-family (*Ischnochitoninae*) are as follows:—*Schizoplax*, Dall; *Tonicella*, *Trachydermon*, and *Dinoplax*, Carpenter; *Callochiton* and *Ischnochiton*, Gray; *Chaetopleura*, Shuttleworth.

Family 2. Mopaliidae. Pilsbry.

Valves externally divided normally into central and lateral areas, the posterior valve with a sinus behind, one or two slits on each side of it or none; intermediate valves each with a single slit; teeth smooth, sharp, often with thickened edges on the outside; girdle more or less hairy. Pleistocene and Recent.

This family comprises the following genera:—*Mopalia* and *Plaxiphora*, Gray; *Placiphorella*, Carpenter; and *Placophoropsis*, Pilsbry

Family 3. Acanthochitidae. Pilsbry.

Valves more or less immersed in the smooth or hairy girdle, the tegmentum therefore much smaller than the articulamentum; the exposed surface divided into a narrow dorsal and wide latero-pleural areas, the latter formed by the union of the lateral and pleural areas of normal Chitons. Insertion teeth sharp, rarely smooth; posterior valve either slit like the head-valve, or having a posterior sinus; head-valve usually with five slits, intermediate valves singly slit. Body never vermiform. Pliocene to Recent.

The following representatives are to be cited:—*Acanthochites*, Risso; *Spongiochiton*, Carpenter; *Katharina* and *Amicula*, Gray; *Cryptochiton*, Midd. and Gray.

Family 4. Cryptoplacidae. Dall.

Elongated or vermiform Chitons with small valves; insertion and sutural plates strongly drawn forward, sharp and smooth; the anterior valve with three to five slits, the others with one slit on each side, or none; tail-valve having the mucro far posterior, insertion plate continuous behind; girdle very thick and wide.

This is a highly specialised branch of a low group of Chitons, unknown in the fossil state. *Cryptoplax*, Blainville (*Chitonellus*, Lam.), and *Choneplax*, Carpenter, are examples.

Sub-Order C. TELEOPLACOPHORA. Pilsbry.

All valves, or the first seven, with insertion plates cut into teeth by slits; the teeth sharply sculptured (pectinated) outside by fine vertical grooves.

Family 1. Chitonidae. Pilsbry.

Characters those of the sub-order. Tertiary and Recent.

The family is illustrated by the following genera, of which only the first two occur in the fossil condition :—*Chiton*, Linné ; *Trachydon*, Dall ; *Eudoxochiton*, Shuttleworth ; *Tonicia*, *Schizochiton*, *Enoplochiton*, and *Onithochiton*, Gray ; *Acanthopleura*, Guilding ; *Loriea*, Adams ; *Loricella* and *Liolophura*, Pilsbry.

Class 4. GASTROPODA. Snails.[1]

Mollusks with distinct head, soled or more rarely fin-like foot, and undivided mantle, which latter secretes a simple, spirally wound, or saucer-shaped shell.

Gastropods differ from Pelecypods in having a more or less distinctly marked head, which usually bears tentacles, eyes, and ears, and contains a

[1] Literature (see also under the head of Mollusca, pp. 344-345) :

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Vinassa de Regny, P. E., Synopsis dei molluschi terziari delle Alpe venete (Palaeontogr. Italica, vols. I., II.), 1896-97.
Harris, G. F., The Australasian Tertiary Mollusca (British Museum Catalogue of Tertiary Mollusca, Part I.), 1897.

large cerebral ganglion. The ventral aspect of the creature is commonly formed by a broad foot; but in the *Heteropoda* this is modified into a vertical, laterally compressed fin; and in the *Pteropoda* it is represented by two wing-like swimming membranes near the head. The base of the foot is sometimes of considerable size, and in some forms (*Strombidae*) the animal is enabled to spring quite a distance by contracting the foot. The mantle lobe is elevated along the back like a hood, extending as far as the head, and usually secretes a shell from its outer surface. The shell covers the intestinal sac and lung cavity, and usually permits of retraction into it of the entire body of the animal. Body and shell are united by muscular attachment; in spiral shells the muscle is fastened to the columella, but in bowl-shaped forms to the inner surface of the shell.

The nervous system consists of two cerebral ganglia, the paired pedal and visceral ganglia, and two or three additional pairs, all of which are united by commissures. A complete crossing of the commissures of the visceral ganglia sometimes takes place (*Chiastoneura*), but in other forms they run parallel (*Orthoneura*).

The peculiar armature of the mouth, although developed in all classes of Mollusks except Pelecypods, is especially characteristic of Gastropods. This consists of two jaw-like horny plates on the upper wall of the oesophagus, opposed to which is a chitinous grating, strap, or *radula*, resting upon the tongue or *odontophore*. The tongue itself is merely a swelling at the bottom of the buccal cavity. The radula is usually quite long, and is beset with innumerable small teeth or hooks, placed in transverse and longitudinal rows. The exceeding diversity of the radula amongst the different groups was advantageously employed by Lovén and Troschel as a basis of their classification.

The oesophagus conducts into a long, coiled, intestinal canal, which is surrounded by a large liver, the kidneys, and numerous glands. The intestine ends in an anal opening placed anteriorly. The heart, as a rule, has one auricle (*Monotocardia*), more rarely two (*Diotocardia*), and serves as a central organ for the supply of a much branched system of blood-vessels. When the gills or lungs are placed in front of the heart (*Prosobranchia*, *Pulmonata*), the auricles are anterior to the ventricle; but when placed behind the heart (*Opisthobranchia*, *Pteropoda*), the auricle is posterior.

Only a few Gastropods breathe through the general surface of the body, and are without distinct organs of respiration; the vast majority possess gills or lungs. The gills are lamellar or tuft-like, sometimes branched or feathered lobes of the integument, and are usually placed in the gill-cavity below the mantle; more rarely they project freely on the back or at the sides. Only exceptionally are they present in large numbers and symmetrically developed; and when so disposed they are always secondary structures not homologous with the normal ctenidia. Typically there are two gills, but the left usually becomes completely atrophied, and the right takes up a median position, consequent upon the torsion of the body, or even migrates over to the left side. Air-breathing snails have the gills replaced by a sac-like cavity, the lung occupying the place of the gill-cavity. The walls of this respiratory cavity are covered with a finely branched network of blood-vessels. The *Ampullariidae* and *Siphonariidae* possess both gills and lungs. The opening of the respiratory cavity is reduced to a round or crescentic aperture, called the

breathing pore. The sides of this pore, in operculated snails, are often produced outwards, so as to form a closed or cleft tube, corresponding with which there is frequently a canal-like process of the shell.

Gastropods are remarkable for their extreme differentiation of the reproductive organs. The sexes are distinct in the *Prosobranchia* and *Heteropoda*, but united in the *Opisthobranchiata*, *Pteropoda*, and *Pulmonata*. The ovarian and seminal ducts of hermaphrodites sometimes open into a common cloaca, or they may terminate in separate openings.

The shell, as has already been remarked, is secreted by the mantle, and is limited in form and size by the configuration of the intestinal sac. It is composed of a chitinous substance (*conchiolin*) infiltrated with lime carbonate, or exceptionally with sulphate of lime in small quantities. Shell characters are of great importance in distinguishing genera and species, but their value in classifying larger groups is comparatively slight, owing to the fact that very similar shells are often developed among forms which differ widely in their general organisation. Two forms of shell-habit occur, the symmetrical and the spiral. The first are flat-, conical, or saucer-shaped, and characterise only a few groups (*Cyclobranchia*, *Aspidobranchia*, *Pulmonata*). Transition forms between the symmetrical and spiral are to be observed in conical shells with slightly inrolled beaks. Exceptional forms of the spiral shell are seen in *Vermetus*, which is irregularly coiled, and in *Planorbis*, *Bellerophon*, and *Atlanta*, coiled in one plane (discoidal). Usually the shell forms a screw-like spiral, and rests upon the back of the creature in such a way that the apex is directed upward and backward, the aperture forward and downward. Holding the shell upright so that the apex is above, and the aperture below, facing the observer, it is said to be right-handed or *dextral* when the opening is on the right side, and left-handed or *sinistral* when on the left side. By far the larger number of Gastropods are dextral; but a few (*Clausilia*, *Physa*, *Spirialis*) are normally sinistral. Right-handed individuals of normally left-handed genera, as well as pathologic individuals of normally right-handed forms, are occasionally met with.

In drawing and describing Gastropod shells, the apex is ordinarily directed upward, so that the right- or left-handedness may be seen at a glance. It is also customary to employ the terms above and below in the same sense as posterior and anterior. The height or length of the shell is measured by a line drawn from the apex to the lower margin of the aperture.

The shell is to be considered as a more or less rapidly widening cone, which is wound either around an axial pillar, called the *columella*, or about a central tubular cavity. Each coil of the tube is termed a *whorl*, and all the whorls except the last one form together the *spire*. The last or body whorl is often very much larger than the preceding; its lower, sometimes flattened surface is called the *base*. As a rule, the whorls are in contact with each other, each in succession either partly or entirely covering the preceding; but in rare cases they form a loose spiral, in which the whorls are separated from one another. The spire is said to be *convolute* when the later whorls entirely conceal the earlier ones, as in *Cypraea*. The line between two contiguous whorls is known as the *suture*. According to the manner of inrolling, various shell contours are produced, requiring numerous descriptive names, such as conical, auriform, turbinate, fusiform, cylindrical, spherical, oval, pyramidal, etc.

When the inner parts of the whorls coalesce to form a columella, the shell is said to be *imperforate;* it is *perforate* when they do not so coalesce, but leave a central tubular cavity instead. The opening of this perforation below, in the centre of the base, is designated the *umbilicus* (Nabel). A true umbilicus reaches to the apex of the shell; when confined to the last whorl only, it is called a false umbilicus. An umbilical fissure is sometimes produced through a partial covering of the umbilicus by the reflected inner lip, or by a shelly growth termed the *callus*.

The aperture is variable in form, being most commonly oval, rounded, crescentic, or half-round, but is sometimes contracted or even fissure-like. Its margin is called the *peristome*, the outer part of which forms the outer lip, and the part next the columella the inner lip. Some shells have a continuous, uninterrupted peristome, but as a rule the inner and outer lips are disconnected. The aperture is said to be entire when rounded anteriorly (inferiorly), as in the *Holostomata;* it is channelled when a basal notch or canal, caused by an inbending of the margin next the base of the columella, is developed. This anterior canal serves for the lodgment of the siphon, as the tube is called which conducts water to the gills; it may be either straight or recurved, and in the *Siphonostomata* it is greatly produced, sometimes even exceeding the aperture in length. The outer lip may be entire or incised, thin and sharp or thickened, curved outward (reflected) or inward (inflected), even or crenulated, or it may be produced into alar or finger-like processes. It is sometimes channelled by a canal at the posterior border, in which the anal or excurrent canal is placed. The upper or posterior portion of the inner margin is commonly designated, especially in the *Siphonostomata*, as the *true inner lip*, in contradistinction from the lower or columellar portion. The inner lip is formed either by the wall of the penultimate whorl, or by a calcareous callus; like the outer lip and columella, it may bear spiral folds, which in some cases extend backward as far as the apex (Fig. 794).

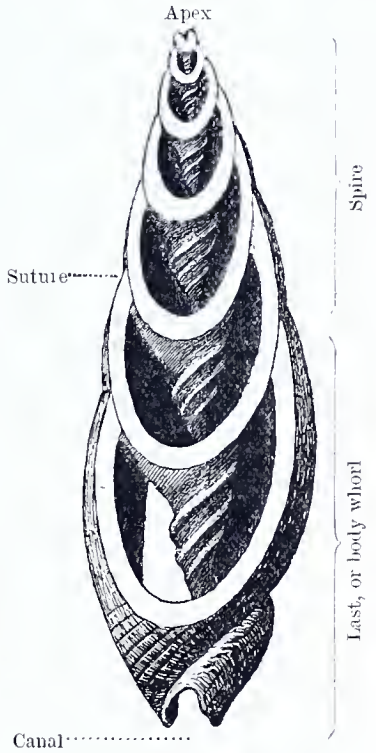


FIG. 794.

Mitra episcopalis, Linn. View of shell sawed through longitudinally, showing columella with folds.

The external ornamentation usually consists of impressed lines or grooves, or of elevated ridges, ribs, folds, nodes, spines, and the like. The markings are called *spiral* when they run parallel with the suture, and *transverse* or longitudinal when they meet the suture at right angles or obliquely. Many Gastropods are brilliantly coloured, others have a velvety or hairy epidermis. The fossilisation process is usually destructive not only of the epidermis, but of the coloration as well.

The essential constituent of univalve shells is aragonite, which usually forms a homogeneous, porcelain-like layer. Many families have in addition to this an inner nacreous layer, which is made up of alternating strata of conchiolin and calcium carbonate, running parallel with the inner surface of

the shell. The porcellanous material is composed of three distinct layers, each of which is made up of thin laminae, and the laminae in turn of very small oblique prisms. The laminae of the middle layer are disposed at right angles to those of the adjacent layers.

Many Gastropods have a calcareous or horny plate, called the *operculum*, attached to the posterior part of the foot, and serving to close the aperture more or less completely when the animal withdraws into its shell. Being most commonly of corneous nature, it is seldom preserved fossil; sometimes, however, it is calcareous, and may attain considerable size and thickness. On the outer surface it may be smooth, furrowed, granulated, or covered with excrescences. The *nucleus* or initial point of growth is sometimes central, and again eccentric or even marginal in position; it may be surrounded by concentric markings, or form the origin of a spiral consisting of few (paucispiral) or many (multispiral) whorls. Certain *Solariidae* have a conical operculum, which is covered externally with numerous spiral lamellae.

The embryonic stages of Gastropods are completed in the egg. Very early in its development the embryo forms a small shell, called the *protoconch* or nucleus, which consists sometimes of several whorls, and not infrequently differs in form from the shell of the adult. The protoconch remains attached to the apex for a time, in the form of a small glistening knob, or a short smooth spire, which occasionally stands at an angle to the rest of the shell, or is even twisted in a contrary direction (heterostrophic). Should the protoconch become decollated, a small calcareous plate closes over the apex of the spire.

All branchiate Gastropods are aqueous in habitat, but there are some forms having a lung cavity which live permanently in fresh water (*Limnaeidae*), and others which are exclusively marine (*Siphonariidae*). The greater number of Gastropods, especially the large and solid forms, frequent the coast-line, and inhabit comparatively shallow water. Some become attached to shoals and plants, others burrow in sand or mud. A great reduction in the Gastropod fauna is noticed at a depth of between 70 and 100 meters, but many genera (*Pleurotoma*, *Fusus*, *Natica*, *Odostomia*, *Eulima*, *Scissurella*, *Turbo*, *Cylichna*, *Tornatina*, *Actaeon*, etc.) persist into the greatest depths yet explored. Most marine Gastropods are killed by removal into fresh water; a few genera, however, are able to maintain their existence in brackish or in fresh water (*Cerithium*, *Littorina*, *Rissoa*, *Trochus*, *Purpura*, etc.). On the other hand, many fresh-water forms (*Melania*, *Melanopsis*, *Neritina*, *Ampullaria*, *Limnaea*, *Planorbis*) can survive in brackish or even strong salt water.

Most Gastropods are herbivorous, but a few subsist upon living or decomposed animal food. Many genera (*Natica*, *Buccinum*, *Murex*) perforate the shells of other Mollusks with their radula, and extract the contents.

Classification.—Ordinal divisions have been based since the time of Cuvier and Milne-Edwards upon the respiratory organs, and the structure of the foot (whether adapted for swimming or crawling). The reproductive organs, and the structure of the heart and nervous system, are also of prime importance. For separating smaller groups, shell characters and the radula are largely employed. Gastropods may be divided into two sub-classes: *Streptoneura*, with the orders *Ctenobranchiata* and *Aspidobranchia*; and *Euthyneura*, with the orders *Opisthobranchia* and *Pulmonata*.

Sub-Class 1. STREPTONEURA. Spengel.

(*Prosobranchia*, Cuvier; *Cochlides*, Ihering.)

Gastropods in which the visceral commissures are crossed, producing an 8*-shaped loop; sexes separate; heart behind the gill; a shell almost always developed, and with few exceptions provided with an operculum.*

The *Streptoneura*, or Prosobranchiates as they are often called, constitute by far the largest group of Gastropods, and comprise at least 20,000 living and fossil species. The shell is usually spiral, more rarely symmetrical, saucer-shaped or conical. The intestinal sac is twisted from left to right, so that the anal opening is placed on the right side near the head, and the organs normally belonging to the right side (kidneys and gills) migrate over to the left. As a rule, only one (the right) of the lamellar gills is fully developed, but in some cases the two are of equal size. The gill veins enter anteriorly into the single or double-aurieled heart.

The large number of Prosobranchiates have been variously classified. Cuvier, Milne-Edwards, and most of the older zoologists laid emphasis upon the number and formation of the gills; Troschel and Lovén upon the characters of the radula; Ihering upon the nervous system; Möreh and more recently Perrier and Bouvier upon the structure of the heart. As none of these characters leave a marked impress upon the shell, they are without practical value in Palaeontology. Nevertheless, the two orders *Aspidobranchia* and *Ctenobranchia* form natural groups, and are recognised, albeit under different names, in all classificatory systems.

Order 1. ASPIDOBRANCHIA. Schweigger.

(*Cyclobranchia* and *Scutibranchia*, Cuvier.)

Nervous system not much concentrated anteriorly; a penis generally absent; radula multiserial.

This group includes most Palaeozoic Gastropods, and is regarded as the most primitive expression of the class. The nervous system and radula are of low, decidedly generalised type, and in some families two symmetrical ctenidia or gills are developed, as in Pelecypods.

Sub-Order A. DOCOGLOSSA. Troschel. Limpets.

(*Cyclobranchia pars*, Cuvier; *Heterocardia*, Perrier.)

Symmetrical, with conic or bowl-shaped non-spiral shells; operculum wanting. Organs of respiration represented either by a ring of laminae (secondary or pallial gills) beneath the mantle margin, or by a comb-shaped true gill in front, anterior to the heart, or by both true and secondary gills. Tongue set with peculiarly modified teeth. Heart with one auricle. Marine. Cambrian to Recent.

The impression of the adductor muscle in the shell cavity is horseshoe-shaped, open in front. In the family *Tryblidiidae*, the horse-shoe is broken into numerous separate impressions. The three families *Patellidae*, *Acmaeidae*, and *Lepetidae* have the impression uninterrupted, and are distinguished by the structure of the gills. The

shells themselves exhibit little variation in form, and hence their generic and even family affinities are almost always doubtful in the fossil state. About 1400 recent limpets are known; these are almost exclusively shallow water inhabitants, and subsist on algae. Fossil forms are uncommon.

Family 1. **Patellidae.** Carpenter.

Patella, Linn. Cup-shaped, round, or oval, depressed conical, with sub-central or eccentric apex. Surface usually with radiating ribs or striae. Silurian to Recent.

Helcion, Montf. Differs in having the beak strongly recurved anteriorly. Eocene to Recent.

Helcioniscus, Dall; *Nacella*, Schum. Recent.

Acmaea, Eschscholtz (*Tectura*, auct., Fig. 795). Like *Patella*, but shell having generally a differentiated marginal band inside; externally smooth, finely striated, or radially ribbed. Beak anterior to the middle. Silurian to Recent. *Lottia*, Gray, is closely allied.

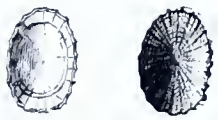


Fig. 795.

Acmaea Raincourti, Desh. Eocene; Auvers, near Paris.

Scurria, Gray (Fig. 796). High conical, smooth, with sub-central beak. Jura to Recent.

Metoptoma, Phil. Depressed conical, with sub-central beak. Posterior side excavated. Silurian to Carboniferous.

Lepetopsis, Whitf. Silurian to Carboniferous.

The genera *Palaeacmaea*, Hall, from the Silurian, and *Scenella*, Billings, from the Cambrian, are the oldest representatives of the *Docoglossa*. They are small, smooth, or radially ornamented, and scarcely to be distinguished from *Acmaea*. *Lepeta*, Gray, and *Lepetella*, Verrill, are small simple limpets of the Recent and late Tertiary, with degenerate, aborted gills.

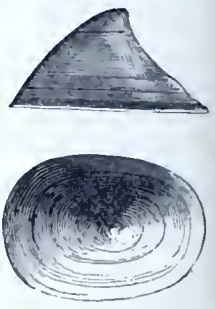


Fig. 796.

Scurria nitida, Deslongch. Great Oolite; Langrune, Calvados. 1/1.

Family 2. **Tryblidiidae.** Pilsbry.

Limpets with the muscle scar broken into numerous separate impressions. Silurian.

Tryblidium, Lindström (Fig. 797). Shell depressed, very thick, oval, with anterior beak; ornamented externally with concentric lamellae. Six pairs of muscle scars arranged in the form of a horse-shoe. Silurian.

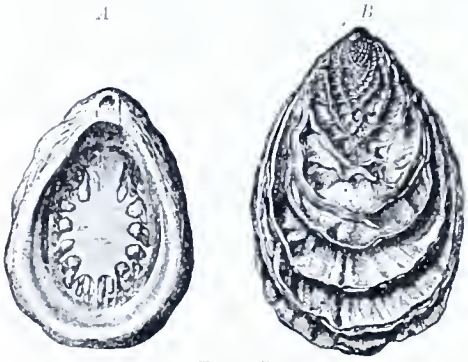


Fig. 797.

Tryblidium reticulatum, Lindström. Silurian; Gottland. *A*, Internal, and *B*, external aspect (after Lindström).

Sub-Order B. **RHIPIDOGLOSSA.** Troschel.

(*Scutibranchiata*, Cuvier; *Zygobranchia*, Ihering; *Diotocardia*, Ihering.)

Symmetrical and limpet-like, or with spiral shells. Gills plume-like, two and symmetrical, or single. Radula with several large plates or teeth in the median portion, and excessively numerous, crowded, narrow, hook-shaped marginal teeth. Operculum often present.

The *Rhipidoglossa* comprise both air-breathing and aquatic forms, and are divisible into two series: *Zygobranchia*, in which two gills are developed, and the shell is generally perforated at the apex or has a slit in the outer lip; and *Anisobranchia*, with a single gill and generally unslit shell.

Family 1. **Haliotidae.** Fleming.

Shell flattened, auriform, with wide aperture, and no operculum. Interior nacreous, with a row of perforations on the left outer margin. Marine. Cretaceous to Recent.

Haliotis, Linn. This, the solitary genus, occurs very rarely fossil except in the Quaternary.

Family 2. **Pleurotomariidae.** d'Orbigny.

Shell spiral, sub-spherical, turbinate, conic, turreted, or planorboid, nacreous internally. Outer lip with a slit, from which a slit-band (the anal fasciole) extends backward, traversing all the whorls. The slit sometimes replaced by one or more perforations. Operculum horny. Cambrian to Recent.

Raphistoma, Hall. Spire depressed or completely flattened; whorls angular above. Umbilicus moderately broad; outer lip with short notch on the keel. Cambrian to Silurian.

Pleurotomaria, Defr. (Figs. 798-802). Shell broadly conical or turbinate; spire sometimes high, in other cases depressed; umbilicus present or absent. Outer lip with slit; growth-lines strongly recurved, meeting in the slit-band. Silurian to Recent. Four living and several hundred fossil species known. Rare in the late Tertiary

Fig. 798.

Pleurotomaria (*Rhaphistomella*) *radians*, Wissm. Keuper; St. Cassian, Tyrol.

Fig. 799.

Pleurotomaria (*Cryptaenia*) *polita*, Goldf. Lower Lias; Göppingen, Wurtemberg.

Sub-genera: *Ptychomphalus*, Agassiz; *Mourlonia*, *Worthenia*, *Agnesia*, de Koninck; *Gosseletina*, *Ivania* (*Baylea*, de Kon.), Bayle; *Raphistomella* (Fig. 798), *Zygites*, *Laubella*, *Stuorella*, *Schizodiscus*, Kittl; *Brilonella*, Kayser; *Hesperiella*, Holzapfel; *Cryptaenia* (Fig. 799), *Leptomaria*, Deslongchamps (Fig. 802), etc.

Fig. 800.

Pleurotomaria bitorquata, Deslongchamps. Middle Lias; May, Calvados.

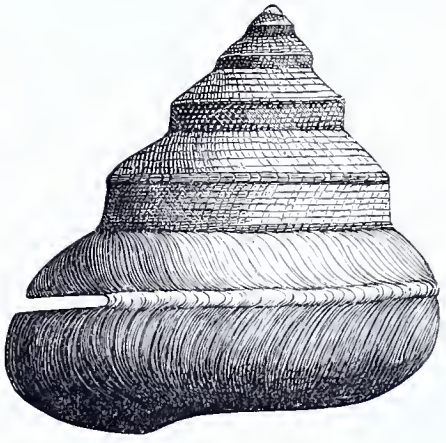


Fig. 801.

Pleurotomaria subscalaris, Deslongchamps. Lower Oolite; Bayeux, Calvados. 1/2.

Porcellia, Leveillé (*Leveilleia*, Newton), (Fig. 803). Shell discoidal, flat, widely umbilicate, nearly symmetrical, and all but the first few whorls coiled in the same

plane. Outer lip sharp, with long slit. Slit-band prominent, traversing the central portion of the whorls. Devonian and Carboniferous.

Kokenella, Kittl. Very flat, discoidal, and only slightly asymmetrical, with a broad slit-band. Trias. *K. Fischeri*, Hoernes sp.

Polytremaria, de Kon. Shell turbinate,

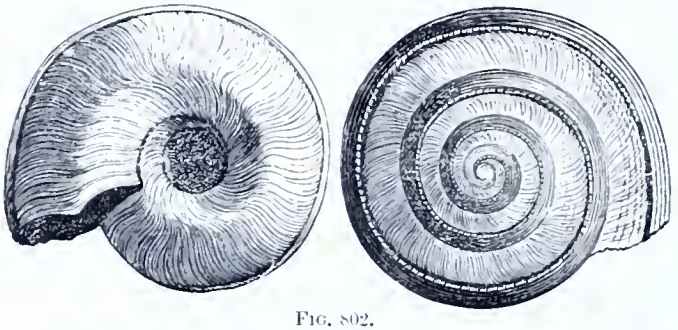


Fig. 802.

Pleurotomaria (*Leptomaria*) *macromphala*, Zittel. Tithonian; Stramberg, Moravia.

Fig. 803.

Porcellia Puzosi, Leveillé. Carboniferous; Tournay, Belgium.

with band replaced by a row of perforations, of which the posterior ones are successively closed. Carboniferous.

Ditremaria, d'Orb. (Fig. 804). Two oval perforations connected by a slit are present behind the outer lip; base with an umbilical callus. Jura.

Trochotoma, Deslongch. Shell turbinate, with conical base. A slit closed at either end is present behind the outer lip, and corresponding to it is a slit-band. Trias and Jura.

Schizogonium, Koken; *Temnotropis*, Laube. Trias. *Cantantostoma*, Sandb. Devonian.

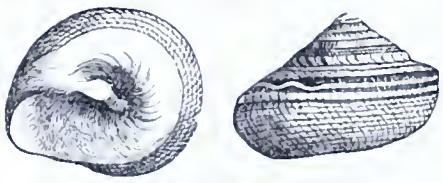


Fig. 804.

Ditremaria granulifera, Zittel. Upper Tithonian; Stramberg, Moravia.

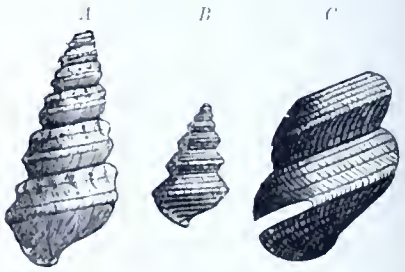


Fig. 805.

A, *Murchisonia bilineata*, d'Arch. and Vern. Devonian; Paffrath, near Cologne. *B*, *M. Blumi*, Klipstein. Trias; St. Cassian, Tyrol. *C*, *M. subsulcata*, de Kon. Carboniferous; Tournay, Belgium. Last two whorls, $^2/_1$.

Murchisonia, d'Arch. and Vern. (Fig. 805). Shell turreted, with numerous smooth or ornamented whorls. Outer lip with a slit, and corresponding to it a slit-band. Cambrian to Trias. Maximum distribution in Devonian and Carboniferous.

Sub-genera: *Hormotoma*, Salter; *Lophospira*, Whitf.; *Goniostropha*, Oehlert; *Cheilotoma*, Koken.

Family 3. **Bellerophontidae**. M'Coy.

Shell bilaterally symmetrical, coiled in one plane, usually quite thick, with weakly developed nacreous layer. Aperture broad, oval, or narrowly elongate. Outer lip with a notch or slit in the middle, corresponding to which is often a band or row of perforations along the whorls. Cambrian to Trias.

The *Bellerophontidae* were classed by Montfort with the *Cephalopoda*, by Deshayes, on account of their resemblance to *Atlanta*, with the *Heteropoda*, and by de Koninck with the Aspidobranchiates. The thick shells sometimes retain traces of their original pigmentation. At least 300 Palaeozoic species have been described.

Bellerophon, Montf. (*Waagenia*, de Kon.), (Fig. 806). Shell globose or discoidal, more or less convolute, and narrowly umbilicate on both sides. Aperture sub-circular or oval, with a deep median sinus; slit-band either distinct or replaced by a keel, sometimes absent. Outer lip sharp, columellar edge often with callus. External surface marked only by growth-lines. Silurian to Permian; maximum in Carboniferous.

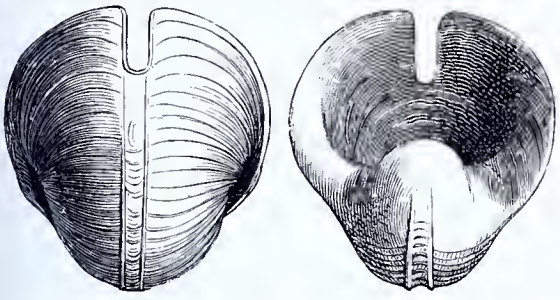


Fig. 806.

Bellerophon bicarenus, Leveillé. Carboniferous; Tournay, Belgium.

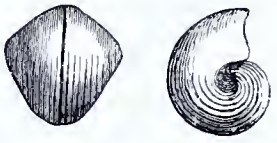


Fig. 807.

Bellerophon (*Euphemus*) *Urii*, Flem. Carboniferous; Edinburg.

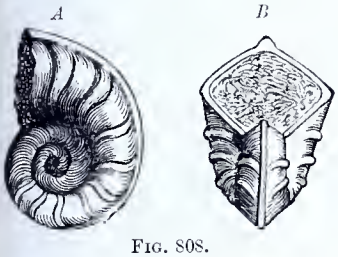


Fig. 808.

Cyrtolites ornatus, Conrad. *A*, Specimen viewed from one side, from Ordovician of Boonville, New York (after F. Roemer). *B*, Anterior aspect of specimen from Ordovician of Cincinnati, Ohio.

Sub-genera: *Bucania*, Hall. Silurian and Devonian. *Warthia*, *Mogulia*, Waagen. Carboniferous.

Euphemus, M'Coy (Fig. 807). Like *Bellerophon*, but the inner whorls, and a part of the last, spirally striated. Carboniferous.

Salpingostoma, Roem. Shell widely umbilicate, the aperture suddenly becoming greatly dilated. Whorls traversed along the middle by a slit closed anteriorly and posteriorly. Silurian and Devonian.

Trematonotus, Hall. Like the last, but the slit-band replaced by a row of perforations. Silurian.

Cyrtolites, Conrad (Fig. 808). Shell widely umbilicate, keeled, without slit, and with strong transverse ribs. Cambrian to Carboniferous.

Family 4. **Fissurellidae**. Risso.

Shell symmetrical, cap- or limpet-shaped, non-nacreous, without operculum. Apex erect or pointing backward, often recurved, perforated. Anterior margin often with a fissure; young shell with a spiral nucleus. Marine; shore forms. Carboniferous to Recent.

Of the three sub-families into which this group is divided, the *Fissurellinae* are known only in the recent fauna. *Fissurellidinae* occur in the Pliocene; all the earlier forms are *Emarginulinae*.

Fissurella, Brug. Shell conical, oval, with an oval apical orifice bounded inside by an entire callus. Recent. The numerous fossil species referred to this genus belong to *Fissuridea*.

Fissurellidea, d'Orb.; *Pupillaea*, Gray; *Megatebennus*, *Lucapinella*, Pilsbry; *Macrochisma*, Swains. These are all recent genera, with the apical orifice very large.

Lucapina, Gray. Like *Fissurella*, but with large apical orifice and finely crenate periphery. Pliocene and Recent.

Fig. 809.

Fissuridea Italica, Defr. Miocene; Grund, Hungary.

Fissuridea, Swains. (*Glyphis*, Cpr.; *Fissurella*, auct.), (Fig. 809). Shell conical, oval, with apex in advance of the middle, giving place to a perforation which is bounded inside by a posteriorly truncate callus. Carboniferous (?) to Recent; very abundant in the Tertiary.

Puneturella, Lowe. Shell conical, with a perforation at or in front of the post-median apex, behind which there is a shelf within the cavity. Eocene to Recent.

Fig. 810.

Emarginula Schlotheimi, Bronn. Oligocene; Weinheim, near Alzey, Baden.

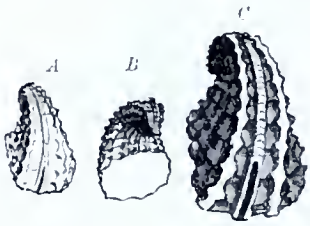


Fig. 811.

Emarginula Muensteri, Pictet. Keuper; St. Cassian, Tyrol. *A*, *B*, Natural size. *C*, Enlarged.

Fig. 812.

Rimula Goldfussi, Roemer sp. Coral-Rag; Hoheneggelsen, Hanover. *A*, Natural size. *B*, Enlarged.

Emarginula, Lam. (Figs. 810, 811). Conical or cap-shaped, with persistent post-median apex, and a slit in the front margin of the shell. Surface cancellated. Carboniferous to Recent.

Rimula, Defr. (Fig. 812). Like the last, but slit replaced by a closed hole on the anterior slope. Lias to Recent.

Subemarginula, Blainv. Like *Emarginula*, but slit short or wanting, and no slit-band. Eocene to Recent.

Scutus, Montf. (*Parmophorus*, Blainv.). Shell depressed, oblong, without fissure, slit, or slit-band; muscle impression near the edge. Eocene to Recent.

The families *Phenacolepadidae*, with the single genus *Phenaeolepas*, Pils. (*Scutellina*, Gray), *Cocculinidae*, and *Addisoniidae* are recent groups allied to the *Fissurellidae*.

Family 5. **Euomphalidae.** de Koninck.

Shell depressed conical to discoidal, spirally coiled, more or less deeply and widely umbilicate. Whorls sometimes in a loose spiral, smooth or angular; the earlier whorls frequently separated off by partitions. Outer lip usually with a shallow indentation. Operculum calcareous. Cambrian to Cretaceous.

The *Euomphalidae* belong primarily to the Palaeozoic era. They have been variously associated with the *Trochidae*, *Turbinidae*, *Littorinidae*, and *Solariidae*. The shells bear a strong resemblance to those of the last-named group, but in *Solarium* the embryonic apex is sinistral, whereas in the *Euomphalidae* it is dextral. Opercula are known with certainty in only a few genera, such as *Maclurea*. de Koninck surmised that the deeply excavated, slipper-shaped opercula from the Carboniferous, described originally as *Calceola Dumontiana*, are referable to *Euomphalus*.

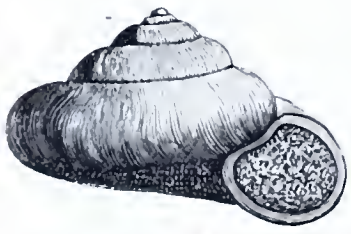


Fig. 813.

Straparollus Dionysii, Montf. Carboniferous; Visé, Belgium.

Straparollina, Billings. Cambrian. *Ophileta*, Vanuxem. Cambrian to Silurian. *Maclurea*, Leseueur. Ordovician and Silurian.

Platyschisma, M'Coy. Thin-shelled, depressed conical, smooth. Umbilicus relatively narrow; outer lip with broad sinus. Silurian to Carboniferous. *P. helicoides*, Sow. Carboniferous.

Straparollus, Montf. (Fig. 813). Turbinate to discoidal, with broad umbilicus. Whorls smooth or with fine transverse striae. Silurian to Jura; especially abundant in Devonian and Carboniferous.

Phanerotinus, Sow. Like the last, except that the whorls form an open spiral. Carboniferous.

Euomphalus, Sow. (*Pleuronotus*, Hall; *Schizostoma*, Bronn), (Fig. 814). Depressed

conical to discoidal, with wide umbilicus. Spire flattened or even concave superiorly; whorls angular, the edges sometimes set with nodes (*Phymatifer*, de Kon.). Outer lip with emargination at the upper angle. Silurian to Trias; maximum in Carboniferous.

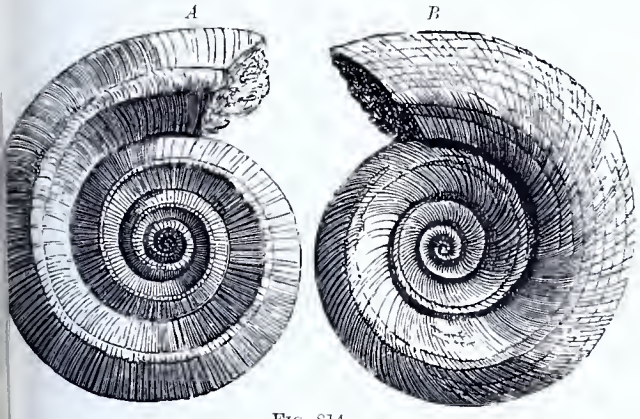


Fig. 814.

Euomphalus catillus, Sowb. sp. Carboniferous; Kildare, Ireland. *A*, Superior, and *B*, Inferior aspect.

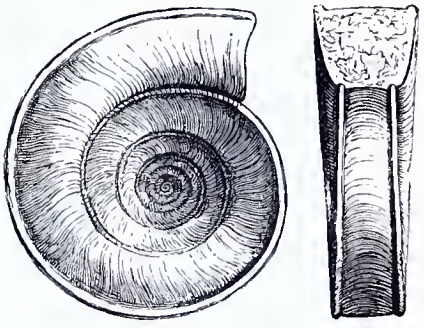


Fig. 815.

Discohelix orbis, Reuss. Middle Lias; Hinter-Schafberg, Austria.

Sub-genera: *Omphalocirrus*, de Ryckholt. Devonian and Carboniferous. *Coelocentrus*, Zittel. Trias.

Discohelix, Dunk. (Fig. 815). Flat, discoidal; upper side flat or slightly concave, the lower widely umbilicate. Whorls rectangular, with sharp edges. Trias to Oligocene.

Family 6. **Stomatiidae.** Gray.

Shell depressed, composed of a few very rapidly widening whorls; nacreous internally; aperture large.

With the exception of *Stomatia*, Helb., and *Stomatella*, Lamarck, a few rare representatives of which are known as early as the Cretaceous (perhaps also Jurassic), this family belongs to the Recent period.

Family 7. **Turbinidae.** Adams.

Shell turbinate, discoidal, or turreted, nacreous internally. Aperture rounded or oval; inner lip smooth or with callus, the outer lip never reflected. Operculum calcareous, very thick, convex externally. Ordovician to Recent.

The extraordinarily abundant recent *Turbinidae* are distinguished principally by characters of the operculum; but inasmuch as this is known in but few of the fossil forms, the precise determination of the latter is usually uncertain. It is customary, therefore, to group under the general head of *Turbo* such fossil turbinate shells with a sub-circular aperture as are not specially distinguished by some other characters.

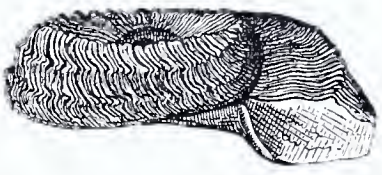


Fig. 816.

Omphalotrochus discus, Sowb. Silurian Dudley, England. 1/1 (after Nicholson).

Fig. 817.

Omphalotrochus globosus, Schloth. sp. Silurian; Gottland. Operculum preserved in place (after Lindström).

Omphalotrochus, Meek (*Polytropis*, de Kon.; *Oriostoma*, Lindström non Munier-Chalm.), (Figs. 816, 817). Discoidal or depressed conical, widely umbilicate. Whorls

round, ornamented with raised longitudinal keels. Operculum extremely thick, flat internally, conical externally, multispiral. Ordovician to Carboniferous; especially abundant in Silurian.

Cyclonema, Hall (Fig. 818). Turbinate; whorls inflated and ornamented with fine spiral striae. Aperture rounded, peristome discontinuous. Operculum conical, flat internally, externally with spiral flutings. Ordovician to Devonian.

Fig. 818.

Cyclonema bilix, Conrad. Ordovician; Cincinnati, Ohio.

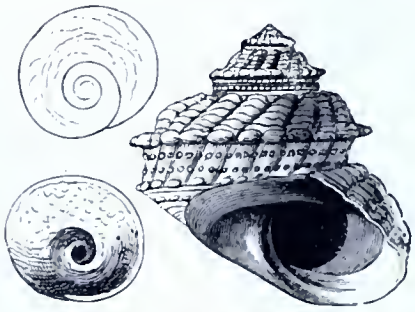


Fig. 819.

Astralium (*Bolma*) *rugosum*, Linn. Pliocene; Pienza, Tuscany. Shell and operculum.

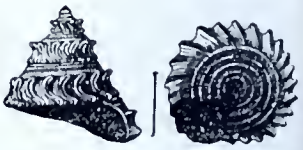


Fig. 820.

Astralium (*Uranilla*) *Damon*, Laube. Keuper; St. Cassian, Tyrol.

Astralium, Link. (Figs. 819, 820). Turbinate; whorls rough, often spinose, and usually keeled. Aperture depressed, with disconnected margin. Base more or less flattened; operculum calcareous, thick, flat internally, spirally coiled, and with very eccentric nucleus. Trias to Recent.

Sub-genera: *Bolma*, Risso (Fig. 819); *Pachypoma*, *Lithopoma*, *Uranilla* (Fig. 820), *Guildfordia*, Gray; *Calcar*, Montfort, etc.

Fig. 821.

Turbo (*Ninella*) *Parkinsoni*, Bast. Oligocene; Dax, near Bordeaux.

Fig. 822.

Collonia modesta, Fuchs. Oligocene; Monte Grumi, near Castel Gomberto, Italy.

Turbo, Linn. (Fig. 821). Turbinate to conical; aperture nearly circular. Operculum calcareous, thick, flat internally, externally convex, multispiral, with sub-central nucleus. Silurian (?) to Recent.

Sub-genera: *Sarmaticus*, *Ninella* (Fig. 821); *Modelia*, *Callopoma*, Gray; *Senectus*, Humphr.; *Batillus*, Schum., etc.

Collonia, Gray (Fig. 822). Like *Turbo*, but operculum with thin calcareous layer disposed in a spiral rib. Eocene to Recent.

Fig. 823.

Phasianella Gosavica, Zekeli. Turonian; Gosau, Austria.

Family 8. **Phasianellidae**. Troschel.

Shell elongated, oval, thin, smooth, lustrous, porcellanous, not nacreous internally, without umbilicus. Body whorl large, with oval aperture. Operculum calcareous, convex externally. Devonian to Recent.

Phasianella, Lam. (*Phasianus*, Montf.), (Fig. 823). With the characters of the family. Cretaceous to Recent; perhaps also Palaeozoic.

Family 9. **Delphinulidae.** Fischer.

Shell turbinate or discoidal, usually thick, nacreous internally, and ornamented externally with spines, ribs, or folds. Aperture circular, peristome entire; outer lip usually expanded or thickened. Operculum horny, often strengthened by a thin calcareous outer layer. Silurian to Recent.

Craspedostoma, Lindström. Globose, narrowly umbilicate, with short spire, and large transversely striated or cancellated body whorl. Inner lip with an alar process at the end of the columella. Silurian. *C. elegantulum*, Lindström.

Crossostoma, Morr. and Lyc. (Fig. 824). Depressed turbinate, smooth, without

Fig. 824.

Crossostoma reflexilabrum, d'Orb. sp. Middle Lias; May, Calvados.

Fig. 825.

Liotia Gervillei, Desh. sp. Calcaire Grossier; Hauteville, near Valogne, France.

Fig. 826.

Delphinula separata, Hèb. Desl. Callovian; Montreuil-Bellay, Maine-et-Loire.

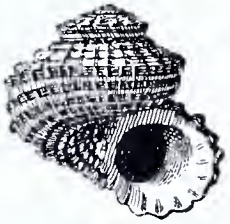


Fig. 827.

Delphinula scobina, Brongt. sp. Oligocene; Gaas, near Dax, France.

umbilicus. Spire short, aperture round, narrowed by a callus. Outer lip somewhat reflexed. Trias and Jura.

Liotia, Gray (Fig. 825). Depressed turbinate, with transverse swellings. Aperture thickened by a callous rim. Jura to Recent.

Delphinula, Lam. (*Angaria*, Bolt.), (Figs. 826, 827). Depressed turbinate, umbilicate. Whorls scaly, spinous, or spirally ornamented. Aperture circular, lip without thickening. Trias to Recent.

Family 10. **Trochonematidae.** Zittel.

Shell pyramidal, turbinate, or discoidal, dextral or sinistral, with internal nacreous layer. Whorls convex, with one or more longitudinal keels, and slightly undulating transverse striae or ribs. Aperture rounded, sometimes with faint notch. Operculum unknown, presumably horny. Marine. Cambrian to Cretaceous.

This extinct group is very abundant in the Palaeozoic, and notably so in Jurassic rocks. The shells, as a rule, are highly ornamented, and have been associated by some with the *Littorinidae*, by others with the *Turbinidae* or *Purpurinidae*. They form a distinct family, which is best placed in the neighbourhood of the *Turbinidae* and *Trochidae*.

Fig. 828.

Eunema strigilata, Salter. Ordovician; Paquette Falls, Canada.

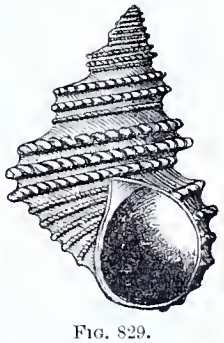


Fig. 829.

Amberleya capitanea, Münst. Upper Lias; La Verpillière, near Lyons, France.

Trochonema, Salter. Pyramidal to turbinate, deeply umbilicate, longitudinally keeled and transversely striated. Aperture round; the umbilicus surrounded by a keel. Cambrian to Silurian.

Eunema, Salter (Fig. 828). Pyramidal, with acute, elongate spire, and no umbilicus. Whorls with two or more spiral keels, and strong transverse striae. Aperture oval, slightly notched anteriorly. Ordovician to Devonian.

Amberleya, Morr. and Lyc. (*Eueyelus*, Deslongch.), (Fig. 829). Turbinate to

pyramidal, with deep sutures, and no umbilicus. Spiral keels usually nodose or spiny, and crossed by strong transverse striae, which are more numerous in the lower portion

Fig. 830.

Platyacra impressa, Schafh. sp. Lower Lias; Hochfellen, Bavaria.

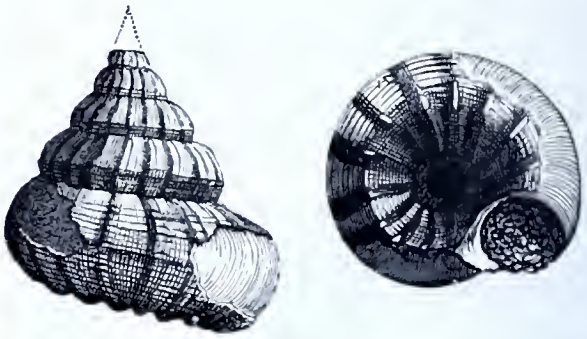


Fig. 831.

Cirrus nodosus, Sowb. Lower Oolite; Yeovil, England.

of the whorls than in the upper. Aperture rounded, sometimes with a shallow notch. Trias to Cretaceous; common in all divisions of the Jura.

Oncospira, Zitt. Pyramidal, spirally ribbed, with one or two transverse swellings on each whorl, disposed continuously along the spire. Jura.

Hamusina, Gemm. Sinistral, with nodose longitudinal keels, and no umbilicus. Lias.

Platyacra, v. Ammon (Fig. 830). Like the last, but with flattened apex, and the earlier whorls discoidal. Lias.

Cirrus, Sow. (*Scaevola*, Gemm.), (Fig. 831). Sinistral, turbinate shells, deeply and widely umbilicate. Spire acuminate; whorls spirally keeled and striated, and with strong transverse ribs. Trias to Middle Jura.

Family 11. **Trochidae.** Adams.

Shell conical, turbinate or pyramidal, nacreous internally. Aperture trapezoidal or sub-circular, peristome disconnected, inner lip often bearing a tooth. Base more or less flattened; operculum thin, horny. Ordovician to Recent.

Precise determination of the numerous fossil *Trochidae* is not less difficult than that of the *Turbinidae*. Palaeozoic and Mesozoic forms in many cases do not harmonise with recent genera, but represent rather collective types, in which characters now distributed amongst several genera or even families are united. Shells incapable of more accurate determination are commonly assigned to the genus *Trochus*. Among the more ancient true *Trochidae* may be mentioned the following:—the *Trochus* species described by Lindström from the Silurian of Gotland; also *Flemingia* and *Glyptobasis*, de Koninck, and *Microdoma*, Meek and Worthen, from the Carboniferous; *Turbina* (Fig. 832) and *Turbonellina*, de Koninck, ranging from the Carboniferous to the Trias.

Fig. 832.

Turbina spiralis, Münst. Keuper; St. Cassian, Tyrol.

Fig. 833.

Trochus (*Tectus*) *Lucasanus*, Brongt. Oligocene; Castel Gomberto, near Vicenza.

Trochus, Linn. (Fig. 833). Shell conical or pyramidal; whorls slightly convex or

flat; base angular at periphery. Inner lip often truncated anteriorly, thickened or with teeth. Silurian to Recent.

Sub-genera: *Tectus*, Montf. (Fig. 833); *Polydonta*, Schum.; *Clanculus*, Montf., etc.

Fig. 834.

Monodonta nodosa, Münst. Keuper; St. Cassian, Tyrol.

Fig. 835.

Monodonta (Oxystele) patula, Brocchi. Miocene; Steinabrunn, near Vienna.

Fig. 836.

Gibbula picta, Eichw. Miocene; Wiesen, near Vienna.

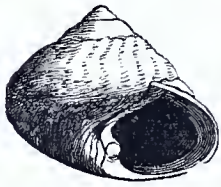


Fig. 837.

Gibbula Broechii, Mayer. Pliocene; Montopoli, Tuscany.

Monodonta, Lam. (Figs. 834, 835). Turbinate, with nearly round aperture, the columella ending below in a tooth. Trias to Recent. In the sub-genera *Osilinus* and *Oxystele*, Phil., the tooth is wanting.

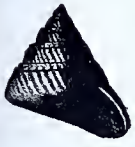


Fig. 838.

Calliostoma semipunctatum, Münst. Keuper; St. Cassian, Tyrol. 2/1.

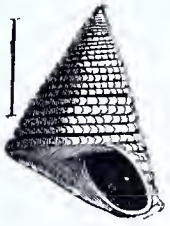


Fig. 839.

Calliostoma aequalis, Buv. Coral-Rag; St. Michiel, Meuse.

Fig. 840.

Lewisiella conica, d'Orb. sp. Middle Lias; May, Calvados.

Fig. 841.

Solariella peregrina, Libassi sp. Pliocene; Orciano, Tuscany.

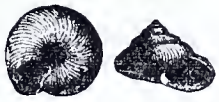


Fig. 842.

Margarita margaritula, Mer. Oligocene; Weinheim, near Alzey, Baden.

Gibbula, Risso (Figs. 836, 837). Turbinate or low conic, umbilicate, and with rounded aperture. Tertiary and Recent.

Calliostoma, Swains. (*Ziziphinus*, Gray), (Figs. 838, 839). Conical, with peripheral keel and flattened base. Trias to Recent.

Other genera are *Cantharidus*, Montfort; *Lewisiella*, Stol. (Fig. 840); *Chlorostoma*, Swains.; *Solariella*, Wood (Fig. 841); *Margarita*, Leach (Fig. 842); *Danilia*, Brus. (Fig. 843), etc. Most of these have a more or less extensive Tertiary history.

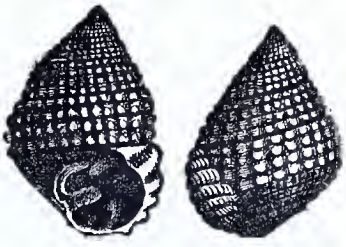


Fig. 843.

Danilia clathrata, Etall. sp. Coral-Rag; Valfin, Ain. 2/1.

Family 12. **Umboniidae**. Adams.

Shell small, usually depressed discoidal, smooth and lustrous, or with fine spiral striae, and without nacreous layer. Outer lip sharp, peristome discontinuous. Umbilicus often concealed by a callus; operculum horny. Silurian to Recent.

Allied to the recent genera *Umbonium*, Link. (*Rotella*, Lam.), *Isanda*, Adams, *Camitia*, Gray, etc., are a number of fossil forms, such as *Pycnomphalus*, Lindström, from the Silurian and Devonian; *Anomphalus*, Meek and Worthen, and *Rotellina*, de

Koninck, from the Carboniferous; *Chrysostoma*, Swainson (Fig. 844), from the Jura, and others, which are probably the ancestors of the *Umbonidae*.

Whether the genera *Teinostoma* (Fig. 845) and *Vitrinella*, Adams, together with their fossil allies from the Carboniferous onward, are rightly assigned to this group, is

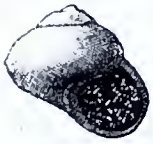


Fig. 844.

Chrysostoma Acmon, d'Orb. sp. Middle Jura; Balin, near Cracow.

Fig. 845.

Teinostoma rotellaeformis, Desh. Calcaire Grossier; Grignon, near Paris.

Fig. 846.

Helicocryptus pusillus, Roem. sp. Coral-Rag; Lindener Berg, near Hannover.

Fig. 847.

Adcorbis tricostatus, Desh. Eocene (Middle Meeressand); Auvers, Seine-et-Oise.

doubtful. *Helicocryptus*, d'Orb. (Fig. 846), from the Jura and Cretaceous, is related to *Vitrinella*. *Cyclostrema*, Marryat, comprising small, lustrous shells; and the spirally striated ones known as *Adcorbis*, S. Wood. (Fig. 847), present strong resemblances to the *Umboniidae*; but, according to Fischer, they form separate families. Both of the last-named genera have fossil representatives in the Tertiary.

Family 13. **Neritopsidae.** Fischer.

Shell oral to semi-globose, with short, sometimes laterally twisted spire, and without umbilicus or nacreous layer. Body whorl very large; aperture oval or semi-circular. Inner lip callous, curved, and occasionally notched. Operculum calcareous, not spiral, with sub-central nucleus, and internally with callous columellar margin, which forms a broad, angular, or rounded process in the middle. Devonian to Recent.

Fig. 848.

Naticopsis Mandelslohi, Klipst. sp. Keuper; St. Cassian.

The *Neritopsidae* are distinguished from the closely related *Neritidae*, principally by the totally different, non-spiral operculum, and by the fact that the earlier whorls are not resorbed, as in the latter family. Detached opercula have been described under the names of *Peltarion*, *Scaphanidia*, *Cyclidia*, and *Rhynchidia*.

Naticopsis, M'Coy (*Neritomopsis*, Waagen), (Figs. 848-850). Shell oval to globose,

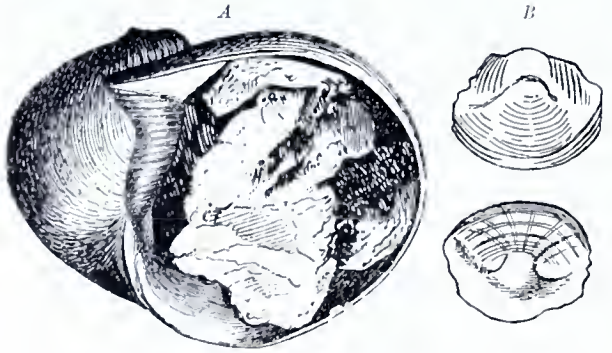


Fig. 849.

A, *Naticopsis ampliata*, Phil. Carboniferous; Visé, Belgium. *B*, Operculum of *N. planispira*, from same locality (after de Koninck).

Fig. 850.

Naticopsis lemniscata, Hoernes. Trias; Esino, Lombardy. Original coloration preserved.

smooth or transversely striated. Aperture oval; inner lip flattened, somewhat

callous, curved, and sometimes transversely striated. Sparse in Devonian, but very common in Carboniferous and Trias.

Hologyra, Koken. Semi-globose, smooth, with faintly impressed sutures. Spire short, laterally situated, not resorbed internally. Inner lip flattened, callous, covering the umbilicus, and with sharp margin. Abundant in the Trias. Some species, such as *H. neritacea*, Münst. sp., have the original colouring admirably preserved.

Marmolatella, Kittl. Auriform to cap-shaped, with very short, incurved, and almost marginal spire. Last whorl much distended; inner lip callous, broad, arched. Trias. *M. (Ostrea) stomatia*, Stopp. sp.; *M. Telleri*, Kittl. sp.

Natiria, de Koninck; Silurian to Carboniferous. *Palaeonarica*, Kittl. (*Pseudofossarus*, Koken).

Naticella, Münst. (Fig. 851). Thin-shelled, depressed, with straight spire, and large, transversely ribbed body whorl. Trias.

Platychilina, Koken (*Fossariopsis*, Laube). Spire depressed, straight; last whorl

Fig. 851.

Naticella costata, Münst. Upper Trias; Wengen, Southern Tyrol.

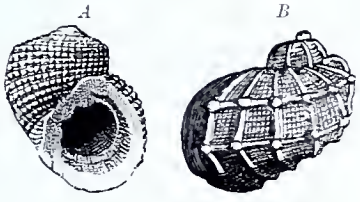


Fig. 852.

A, *Neritopsis moniliformis*, Grat. Miocene; Lapugy, Transylvania. *B*, *N. spinosa*, Heb. Deslong. Callovian; Montreuil-Bellay, Maine-et-Loire.

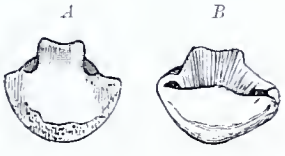


Fig. 853.

Neritopsis radula. Recent; New Caledonia. *A*, External, and *B*, internal aspect (after Crosse). 1/1.

large, surface rough, tuberculose. Inner lip even, with simple margin. Trias. *P. pustulosus*, Münst. sp.

Delphinulopsis, Laube. Like the last, but spire composed of loosely connected whorls. Sutures deep. Body whorl with nodose longitudinal keels. Inner lip even, with sharp margin. Trias. *D. binodosa*, Münst. sp.

Neritopsis, Grat. (Figs. 852, 853). Spire depressed, body whorl very large. Surface with spiral and transverse ribs or nodes, often cancellated. Inner lip thickened, with broad, angular emargination in the middle. Trias to Recent.

Family 14. **Neritidae**. Lamarck.

Shell semi-globose, without umbilicus or nacreous layer. Spire very short, somewhat lateral; whorls rapidly broadening, the last very large, and earlier ones resorbed internally. Aperture semi-circular; margin of the flattened or calloused inner lip often with teeth. Operculum calcareous, with a lateral spiral nucleus, and a process for muscle attachment on the inner side. Trias to Recent.

The *Neritidae* are partly marine, and partly fresh-water inhabitants. The former live usually in the vicinity of the coast, the latter often in brackish water. Since the earlier whorls are internally resorbed, casts reveal no trace of the spire. This character, together with the form of the operculum, serves to distinguish the family from the *Naticopsidae*, from which both it and the terrestrial *Helicinidae* are probably descended. Fossil forms not infrequently retain traces of their former coloration.

Neritaria, Koken (*Protonerita*, Kittl). Spire acuminate, suture deep, surface smooth. Outer lip sharp; inner lip callous, flattened. Resorption of the inner walls incomplete. Trias.

Nerita, Linn. (Fig. 854). Thick, ovoid, or semi-globose, imperforate. Surface smooth or with spiral ribs. Inner lip callous, flattened, with a straight, often denticulate border. Operculum sub-spiral. Trias (?) to Recent.

Oncochilus, Pethö (Fig. 855). Smooth; inner lip arched, callous, bearing two or three teeth on the margin or smooth; outer lip sharp. Trias and Jura.

Lissochilus, Pethö (Fig. 856); *Neritodomus*, Morr. and Lyc.; *Neritoma*, Morris, Jura. *Otostoma*, d'Arch.; *Dejanira*, Stol. Cretaceous.

Velates, Montf. (Fig. 857). Depressed conical, only the curved apex of the spire

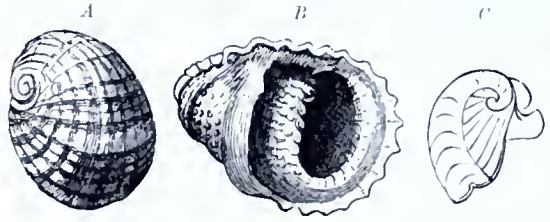


Fig. 854.

A, *Nerita Laffoni*, Merian. Citharella Limestone; Epfenhofen, near Schaffhausen, Switzerland. *B*, *N. granulosa*, Desh. Eocene (Sables Moyens); Auvers, near Paris. *C*, Operculum of a recent *Nerita*.

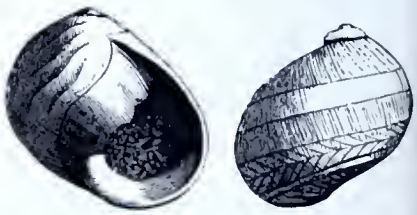


Fig. 855.

Oncochilus chromaticus, Zittel. Upper Tithonian; Stramberg, Moravia.

visible. Last whorl very large. Inner lip convex or straight, with denticulate margin. Abundant in the European Eocene; sometimes attaining a size of 10 or 12 cm.

Neritina, Lam. (Fig. 858). Small, semi-globose, lustrous, smooth or spiny, mostly brilliantly coloured. Inner lip flattened, with sharp or finely toothed margin; outer

Fig. 856.

Lissochilus sigaretinus, Buv. Coral-Rag; Hohenegglsen, Hannover.

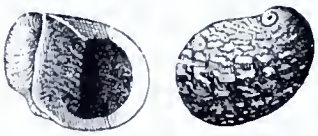


Fig. 858.

Neritina Grateloupana, Fer. Miocene; Häufelburg, near Gimzburg.

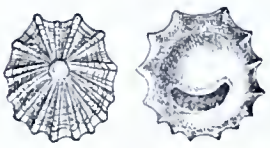


Fig. 859.

Pileolus plicatus, Sowb. Bathonian; Langrune, Calvados. 3/1.

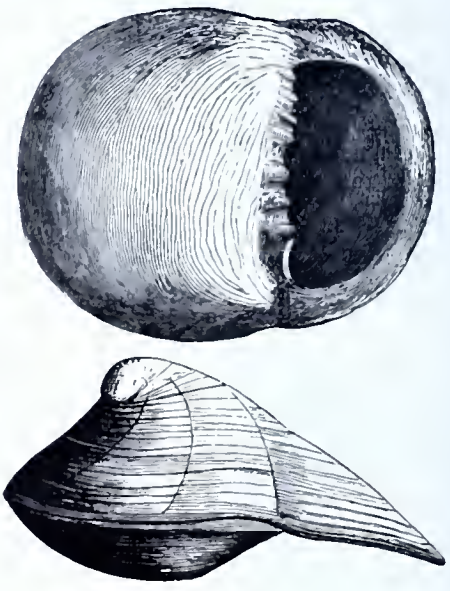


Fig. 857.

Velates Schmidelianus, Chem. Eocene (Lower Meeressand); Cuise-la-Mothe.

lip sharp. Inhabits brackish or fresh water. Abundant in Tertiary and Recent. The supposed Mesozoic forms belong principally to *Nerita*.

Pileolus, Sowb. (Fig. 859). Small, cup-shaped to depressed conical, ovoid or round. Apex slightly curved backwards; only the last whorl visible. Aperture semi-circular; inner lip broad, callous. Jura to Eocene.

Order 2. CTENOBRANCHIATA. Schweigg.

(*Pectinibranchia*, Cuvier; *Azygobranchia*, Ihering; *Monotocardia*, Bouvier.)

Right cervical gill pectinate, very large, and usually transposed to the left side, owing to torsion of the body; the left gill atrophied. Heart with but one auricle. Radula small, variously constructed, but usually armed with few teeth in a transverse series. Shell coiled in a more or less elevated spiral, rarely cup- or cap-shaped.

The *Ctenobranchiata* constitute the largest group of the *Streptoneura*. They are for the most part marine, but some are terrestrial, and some inhabit fresh water. Beginning in the Silurian, they attain their maximum distribution in the Mesozoic, Tertiary, and Recent periods. A division into two groups—*Holostomata* and *Siphonostomata*—according to the nature of the aperture, has been attempted; but this is unnatural, since it emphasises a shell character which is unaccompanied by any anatomical differences. Classifications based upon the structure of the radula, such as have been proposed by Troschel, and more recently by Bouvier, are valueless in Palaeontology. Here it will be sufficient to recognise two sub-orders primarily: *Platypoda*, in which the foot is normally developed; and *Heteropoda*, in which it is modified into a fin.

Sub-Order A. HETEROPODA. Lamarck.

(*Nucleobranchiata*, Blainville.)

To the *Heteropoda* belong naked or shell-covered, free-swimming and pelagic marine Mollusks, with distinct head and highly developed sense organs. Heart, gills, reproductive organs, and nervous system agree with the corresponding organs of the Ctenobranchiates; the radula resembles that of the *Taenioglossa*. They differ considerably, however, from the Prosobranchiates, since the foot is modified into a sort of vertical fin, and imparts to them a peculiar appearance. They rise usually toward evening in great swarms to the surface of the ocean, where they hover about with a very rapid motion, swimming in an inverted position, with the dorsal side down, and the foot uppermost. They are exceedingly delicate, often transparent organisms. The body may be either entirely naked or provided with a very thin, light shell.

Fig. 860.

Atlanta Peronii, Lesueur. Recent; Atlantic Ocean.

Two recent genera have been found also in early Tertiary deposits. Of these *Carinaria*, Lamarck, has a keeled, cap-shaped, glassy shell; while in *Atlanta*, Lesson (Fig. 860), the delicate shell is coiled spirally in a single plane, and the aperture is provided with a slit. Owing to the great similarity of *Atlanta* and *Oxygyrus* to certain Palaeozoic *Bellerophontidae*, a relationship between the two has been not unplausibly suggested. The latter forms are distinguished principally by their heavier, thicker shells.

Sub-Order B. PLATYPODA.

Superfamily 1. GYMNOGLOSSA.

More or less completely parasitic forms, in which the radula is unarmed through degeneration.

Family 1. **Eulimidae.** Fischer.

Small, polished, elongate-conic shells, with ovate apertures; the axis often distorted; nucleus dextral. Trias to Recent.

FIG. 861.

A, Eulima, subulata, Don. Pliocene; Coroncina, Tuscany. *B, E. polita*, Linn. Miocene; Niederleis, Moravia.

FIG. 862.

Niso eburnea, Risso. Pliocene; Monte Mario, near Rome.

Eulima, Risso (Fig. 861). Turreted, smooth, lustrous, without umbilicus. Trias to Recent.

Niso, Risso (Fig. 862). Like the last, but with deep umbilicus reaching to the apex. Trias to Recent.

Family 2. **Pyramidellidae.** Gray.

Shell turreted to elongate-oval. Aperture oval, anteriorly rounded, or with faint canal; outer lip sharp. Operculum horny, spiral. Marine. Cambrian to Recent.

The nucleus consists of several whorls, and in Palaeozoic and Mesozoic forms is coiled in the same direction as the remainder of the shell. But in the younger and more typical genera it is heterostrophic, distinctly separated from the rest of the shell, and often stands at an angle with the adult spire. It is questionable whether forms older than the Cenozoic can be retained in this family; Fischer places most of them in a new family, entitled *Pseudomelaniidae*.

Macrocheilus, Phil. (*Macrochilina*, Bayle; *Strobaeus*, de Kon.), (Fig. 863). Elongate-oval, without umbilicus, smooth or with slightly curved growth-lines. Spire acuminate, only moderately high; last whorl large. Aperture angular posteriorly, sometimes with shallow anterior canal. Inner lip with weak anterior folds. Silurian to Trias.

FIG. 863.

Macrocheilus arculatus, Schloth. sp. Middle Devonian; Paffrath, near Cologne.

? Ptychostoma, Laube; *? Undularia*, Koken. Trias.

Loxonema, Phil. Turreted, whorls arched, with S-shaped growth-lines. Sutures deep; aperture higher than wide, with shallow canal. Silurian to Trias; particularly abundant in the Carboniferous.

FIG. 864.

Pseudomelania Heddingtonensis, Sowb. sp. Oxfordian; France. Bands of original coloration still showing.

FIG. 865.

Pseudomelania (Bayania) lactea, Lam. sp. Calcaire Grossier; Grignon, near Paris.

Zygopleura, Koken. Like the last, but whorls with sharp, slightly curved transverse ribs, or transverse nodose keel. Devonian to Lower Cretaceous.

Bourgetia, Desh. (*Pithodea*, de Kon.). Large, elongate-oval to turreted, with large, inflated body whorl. Surface marked with spiral striae or furrows. Carboniferous and Upper Jura.

Pseudomelania, Pictet (*Chemnitzia*, p.p. d'Orb.), (Fig. 864). Turreted, with numerous, almost flat whorls, and slightly impressed sutures. Surface smooth, or marked by fine growth-lines; aperture rounded anteriorly, or with faint canal. Umbilicus wanting; rarely an umbilical fissure present. Very abundant in the Trias and Jura, less so in Cretaceous and Eocene; probably present also in the Carboniferous.

Sub-genera: *Oonia, Microschiza*, Gemm.; *Hypsipleura, Anoptychia*, Koken. Trias and Jura. *Coelostylina, Eustylus, Spirostylus*, Kittl. Trias. *Bayania*, Munier-Chalm. Eocene. (Fig. 865.)

Pustularia, Koken. Turreted, with groove-like sutures. Whorls flat, with three or more spiral rows of nodes. Trias.

Catosira, Koken. Whorls flat, with transverse ridges. Aperture canaliculate; base with spiral grooves. Trias and Jura.

Diastoma, Desh. (Fig. 866). Like the last, but aperture separated from the body whorl. Whorls with transverse folds and spiral striae. Cretaceous and Tertiary.

Mathilda, Semper (*Promathilda*, Andreae). Turreted; whorls transversely and spirally striated or ribbed. Aperture with canal. Nucleus heterostrophic. Jura to Recent.

Keilostoma, Desh. (*Paryphostoma*, Bayan), (Fig. 867). Turreted, spirally striated. Outer lip with externally thickened margin. Eocene.

Turbonilla, Risso (*Chemnitzia*, p.p. d'Orb.), (Fig. 868). Small, turreted, with heterostrophic nucleus. Whorls transversely ribbed or smooth. Inner lip straight, or occasionally with folds. Tertiary and Recent.

Odontostoma, Fleming (Fig. 869); *Pyramidella*, Lamarck (Fig. 870). Cretaceous to Recent. *Syrnola*, Adams; *Eulimella*, Fischer. Tertiary and Recent. *Palaeoniso*, Gemm. Trias and Jura.

Fig. 866.

Diastoma costellata, Lam. sp. Calcaire Grossier; Damery, near Epernay.

Fig. 867.

Keilostoma turriculu, Brug. sp. (*Melania marginata*, Lam.); Calcaire Grossier; Grignon, near Paris.

The genera *Subulites*, Conrad (? *Polyphemopsis*, Portlock), from the Cambrian to Carboniferous; *Fusispira*, Hall, Ordovician; and *Soleniscus*, Meek and Worthen, Carboniferous, are characterised by narrow, anteriorly elongated and canaliculate apertures. They probably form a separate family, in which also should be placed the Triassic *Euchrysalis*, Laube (Fig. 871).

Fig. 868.

Turbonilla rufa, Phil. Crag; Sutton, England.

Fig. 869.

Odontostoma plicata, Montf. sp. Upper Oligocene; Nieder-Kaufungen, near Cassel.

Fig. 870.

Pyramidella plicosa, Bronn. Miocene; Niederleis, Moravia.

Fig. 871.

Euchrysalis fusiformis, Münst. sp. Trias; St. Cassian, Tyrol.

Superfamily 2. **PTENOGLOSSA.** Gray.

Teeth of the radula subulate, numerous, and similar in each transverse row.

Family 1. **Scalariidae.** Broderip.

Shell turreted, usually narrowly umbilicate. Whorls convex, transversely ribbed or striated. Aperture round, with entire peristome. Operculum horny, paucispiral. Marine. Silurian to Recent.

Holopella, M'Coy (*Aclisina*, de Kon.). Slender, turreted; whorls with fine transverse striae, sometimes cancellated. Silurian to Carboniferous.

Callonema, Hall (*Isonema*, Meek and Worth). Turreted, oval to globose; whorls covered with lamellate transverse ribs; aperture circular. Silurian and Devonian.

Scoliostoma, Braun. Devonian. *Chiloeyclus*, Bronn (*Cochlearia*, Braun). Trias.

Fig. 872.

Scalaria lamellosa, Brocchi. Miocene; Baden, near Vienna.

Scalaria, Lam. (*Scala*, Klein; *Cirsotrema*, Mörch.), (Fig. 872). Turreted; whorls strongly arched, with transverse ribs, and often also spirally striated. Aperture round, outer lip sometimes thickened. Trias to Recent.

Family 2. **Solariidae.** Chenn.

Shell depressed conical, deeply and broadly umbilicate, without nacreous layer. Whorls angular; operculum horny or calcareous, spiral. Embryonal spire heterostrophic. Marine. Cretaceous to Recent.

Fig. 873.

Solarium simplex, Bronn. Miocene; Niederleis, Moravia.

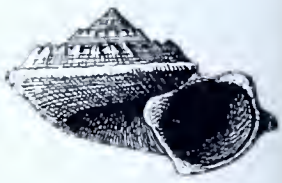


Fig. 874.

Solarium Leymeriei, Ryckholt. Tourtia (Upper Cretaceous); Tournay, Belgium.

The *Solariidae* exhibit some resemblance to the *Euomphalidae*, from which they are distinguished principally by the heterostrophic nucleus.

Solarium, Lam. (Figs. 873, 874). Aperture quadrilateral; operculum horny; umbilical angle notched or sharp. Jura to Recent. A number of Mesozoic forms confused with this genus probably belong to *Euomphalus*.

Torinia, Gray. Tertiary and Recent. *Bifrontia*, Desh. (*Omalaxis*, Desh.). Eocene.

Superfamily 3. **TAENIOGLOSSA.** Bouvier.

Teeth of the radula seven in each transverse row. Mainly holostomate forms, but some genera have deeply notched apertures, as in the higher divisions.

Fig. 875.

Purpuroidea nodulata, Young and Bird sp. Great Oolite; Minchinhampton, England.

Family 1. **Purpurinidae.** Zittel.

Thick-shelled, oval, with platform-like spire, and without pearly layer. Whorls flattened beneath the suture and angular, the angles often beset with nodes. Body whorl large; aperture oval, with anterior emargination, and discontinuous peristome. Operculum unknown. Ordovician to Cretaceous.

Sealites, Conrad. Spire short and acuminate; whorls flattened superiorly and bounded by a sharp angle at the suture. Body whorl very large, smooth; aperture faintly notched. Ordovician (Chazy); according to Laube, also Triassic.

Trachydomia, Meek and Worth (*Trachynerita*, Kittl); *Pseudoscalites*, Kittl; *Tretospira*, Koken. Trias. *Brachtrema*, Morris and Lyc.; *Tomocheilus*, Gemm. Jura.

Purpurina, d'Orb. Elongate-oval. Whorls angular superiorly, spirally ribbed, with transverse folds or costae, highly ornamented, often with umbilical fissure. Aperture oval, anteriorly notched. Rhaetic and Jura.

Purpuroidea, Lycett (Fig. 875). Spire with successive steps or platforms, the

flattened surface beneath the suture bounded by a row of nodes. Last whorl inflated, smooth. Aperture anteriorly with canal-like notch; outer lip thin. Jura and Cretaceous.

Brachytrema, Morris and Lycett; *Tomocheilus*, Gemm. Jura.

Family 2. **Littorinidae.** Gray.

Shell turbinate, usually smooth or spirally ornamented, without nacreous layer. Aperture rounded; outer lip sharp. Operculum horny, paucispiral. Marine. Ordovician to Recent.

Fossil shells of this family are distinguished solely from those of the *Turbinidae* and *Trochidae* by the absence of a pearly layer. The animal, however, differs radically. The heart has but one auricle in the *Littorinidae*, two in the *Turbinidae* and *Trochidae*. The radula in the last-named groups is rhipidoglossate; in the present family it is taenioglossate. The differences in essential structure are thus seen to be considerable; yet the shells when fossilised are so similar, it can scarcely be doubted that the so-called Palaeozoic *Littorinidae* are in many cases very closely related to genera referred to the *Turbinidae* and *Trochidae*. The limits of these families are therefore very uncertain, so far as Palaeozoic forms are concerned. Among the extinct genera which exhibit great similarity to *Littorina*, but are often assigned to the above-named families, may be mentioned the following:—*Holopea*, Hall; Ordovician to Devonian. *Turbonitella*, de Koninck (Fig. 876); Devonian and Carboniferous. *Portlockia*, *Turbinilopsis*, and *Rhabdopleura*, de Koninck; from the Carboniferous. *Lacunina*, Kittl; Trias.

Fig. 876.

Turbonitella subcostata, Goldf. sp. Middle Devonian; Paffrath, near Cologne.

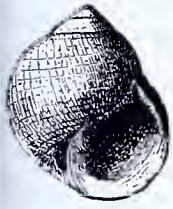


Fig. 877.

Littorina littorea, Linn. sp. Post-Pleistocene; Isle of Skaptö.

Fig. 878.

Lacuna Basterotina, Bronn. Miocene; Steinabrunn, near Vienna.

Fig. 879.

Fossarus costatus, Brocchi. Pliocene; Limite, Tuscany.

Littorina, Fer. (Fig. 877). Thick-shelled, turbinate to globose, smooth or spirally striated, without umbilicus. Aperture oval. Jura to Recent.

Lacuna, Turton (Fig. 878). Like the last, but with a narrow umbilical fissure. Tertiary and Recent.

Lacunella, Desh.; Eocene. *Litiopa*, Rang; *Planaxis*, Lam.; *Quoyia*, Desh.; Tertiary and Recent. The families *Litopidae* and *Planaxidae* are usually recognised.

The genus *Fossarus*, Phil. (Fig. 879), forms, according to Fischer, a separate family, *Fossaridae*. It occurs in the late Tertiary and Recent.

Family 3. **Cyclostomidae.** Menke.

Shell extremely variable in form, turbinate to discoidal, sometimes turreted, covered with epidermis. Aperture circular, with usually entire peristome. Operculum horny or calcareous, spiral. Terrestrial. Cretaceous to Recent.

Like the pulmonate snails, the animal possesses a respiratory cavity. But in other respects they approach the *Littorinidae* very closely, which latter forms also have the gill much reduced. The shell habit is excessively variable. There are more than 600 recent species distributed throughout all parts of the globe, but the majority

of these are tropical. Fossil forms are found in fresh-water deposits as old as the Middle Cretaceous.

Cyclostoma, Lam. (Fig. 880). Turbinate, with calcareous spiral operculum. Tertiary and Recent.

Otopoma, *Tudora*, Gray. Tertiary and Recent.

Megalomastoma, Guild. Turbinate to chrysalis-shaped, usually smooth. Peristome with thick margins; outer lip reflected. Operculum horny. Cretaceous to Recent. *M. mumia*, Lam. sp.

Fig. 880.

Cyclostoma bisulcatum, Zieten. Miocene; Ermingen, near Ulm, Wurtemberg.

Fig. 881.

Pomatias labellum, Thomas sp. Helix Beds (Upper Oligocene); Hochheim, near Wiesbaden.

Fig. 882.

* *Cyclotus exaratus*, Sandb. Upper Eocene; Pugnello, Italy. Shell and operculum (after Sandberger).

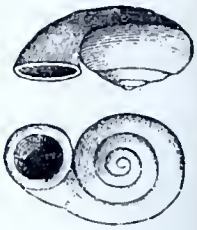


Fig. 883.

Strophostoma anomphala, Capellini. Oligocene; Arnegg, near Ulm, Wurtemberg.

Pomatias, Studer (Fig. 881). Turreted, transversely striated, with reflected margins and calcareous operculum. Tertiary to Recent; palaearctic.

Leptopoma, Pfeiff.; *Cyclophorus*, Montf.; *Craspedopoma*, Pfeiff.; *Cyclotus*, Guilding (Fig. 882), etc. Upper Cretaceous. These genera are considered to form a distinct family, *Cyclophoridae*. *Strophostoma*, Desh. (Fig. 883); Upper Cretaceous to Miocene.

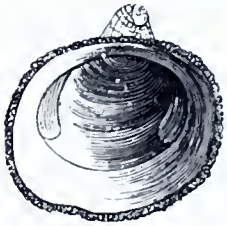


Fig. 884.

Capulus hungaricus, Linn. sp. Pliocene; Tuscany.

Fig. 885.

Capulus rugosus, Sowb. sp. Great Oolite; Langrune, Calvados. 1/1.

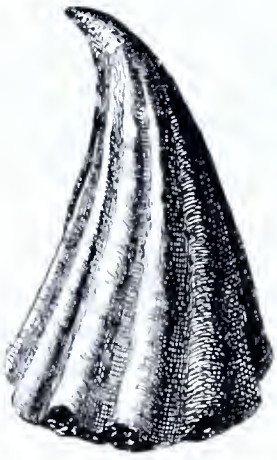


Fig. 886.

Orthonychia elegans, Barr. Silurian (Étage E); Lochkow, Bohemia.

Family 4. **Capulidae**. Cuvier.

Shell cup-, cap-shaped, or oval, irregular, with spirally twisted apex; in some cases the shell is composed of several depressed whorls. Body whorl very large; aperture wide; operculum absent. Marine. Cambrian to Recent.

Various genera belonging here are stationary, remaining throughout nearly the whole of their existence attached to some foreign body, to which they gradually become accommodated in form.

Stenotheca, Salter. Shell small, cap-shaped, concentrically striated or furrowed, with slightly incurved apex, which latter is distantly situated posteriorly. Lower Cambrian.

Capulus, Montf. (*Pileopsis*, Lam.; *Brocchia*, Bronn), (Figs. 884, 885). Irregularly conical or cap-shaped; apex greatly displaced backward, more or less spirally inrolled. Aperture wide, rounded or irregular; internally with a horseshoe-shaped muscular impression. Exceedingly abundant from the Cambrian to Carboniferous, but rather sparse from the Trias onward.

Orthonychia, Hall (*Igoceras*, Hall), (Fig. 886). Shell conical, straight, or slightly curved, often plicated. Apex but faintly spiral. Silurian to Carboniferous.

Platyceras, Conrad (*Acroculia*, Phil.), (Fig. 887). Apex bent and spirally inrolled. Surface smooth, striated, plicated, or covered with small spines. Cambrian to Trias. The fusion of this genus with *Capulus*, as proposed by some authors, is hardly justifiable.

Platyostoma, Conrad (*Strophostylus*, Hall), (Fig. 888). Shell composed of numerous rapidly widening whorls. Spire low, body whorl very large. Inner lip reflected and somewhat thickened. Aperture round, of large size. Silurian to Carboniferous.

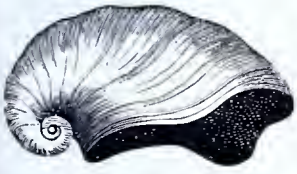


Fig. 887.

Platyceras neritoides, Phil. Carboniferous; Visé, Belgium.

Fig. 888.

Platyostoma niagarensis, Hall. Devonian; Waldron, Indiana.

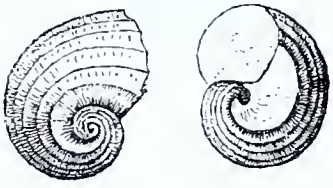


Fig. 889.

Horiostoma Barrandei, Mun.-Chalm. Lower Devonian; Gahard, Ille-et-Vilaine (after Munier-Chalmas).

Horiostoma, Munier-Chalm. (Fig. 889). Shell thick, spirally ribbed, with short lateral spire, and wide umbilicus. Devonian.

Tubina, Barr. Silurian. *Rothpletzia*, Simonelli. Tertiary.

Hipponyx, Defr. (*Cochlolepas*, Klein), (Fig. 890). Shell thick, obliquely conical to cup-shaped. Beak straight, rarely spiral, greatly removed posteriorly. Aperture oval or rounded, internally with a horseshoe-shaped muscular impression. The foot often secretes a thick, operculiform calcareous disc. Cretaceous to Recent.

Galerus, Gray (*Calyptraea*, p.p. Lam.). Shell thin, conical, with central spiral apex. Whorls flattened, often spinose. Base horizontal; aperture wide, depressed. Cretaceous to Recent.

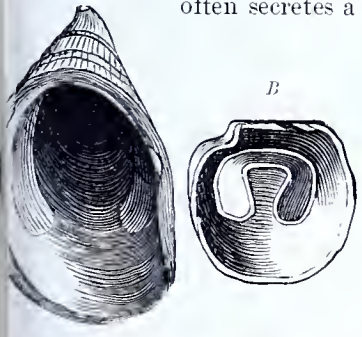


Fig. 890.

Hipponyx cornucopiae, Lam. Calcaire Grossier; Liancourt, near Paris. *A*, Shell. *B*, Foot-plate.

Fig. 891.

Crepidula unguiformis, Lam. Pliocene; Tuscany.

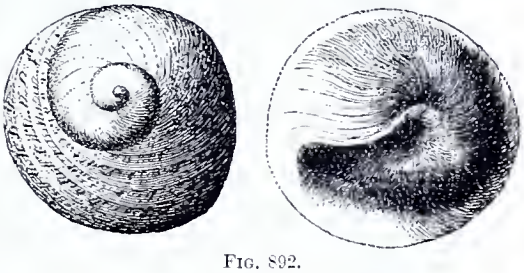


Fig. 892.

Calyptraea trochiformis, Lam. Calcaire Grossier; Damery, near Epernay.

Crepidula, Lam. (Fig. 891). Slipper-shaped, elongate-oval, flat or arched. Beak at the posterior end, almost marginal, somewhat curved. Aperture greatly elongated, wide; inner lip formed by a thin horizontal lamella. Cretaceous to Recent.

Crucibulum, Schum.; *Calyptraea*, Lam. (Fig. 892). Tertiary and Recent.

Family 5. **Naticidae**. Forbes.

Shell with short spire and large body whorl. Aperture semi-circular to oval, angular posteriorly, broadly rounded anteriorly. Operculum calcareous or horny, paucispiral. Marine. Trias to Recent.

The distinction of fossil *Naticidae* from *Naticopsis*, *Nerita*, and *Ampullaria* is

attended with great difficulty, since they frequently possess nearly identical characters in common, differing mainly in the operculum, which is not preserved fossil.

Fig. 893.

Sigaretus haliotoidius, Linn. sp. Miocene; Grund, Hungary.

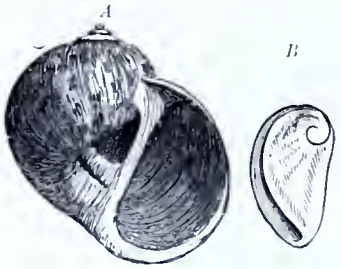


Fig. 894.

A, *Natica millepunctata*, Lam. Pliocene; Monte Mario, near Rome. *B*, Operculum of *N. multipunctata*, S. Woodw. Crag; Sutton.

Fig. 895.

Natica (*Ampullina*) *patula*, Lam. Calcaire Grossier; Damery, near Epernay

Sigaretus, Lam. (Fig. 893). Shell depressed, auriform, spirally striated or furrowed. Spire very low, with rapidly widening whorls. Aperture greatly distended; operculum horny. Tertiary and Recent.

Natica, Lam. (Figs. 894-897). Globose, semi-globose, ovate or pyramidal, smooth and lustrous, rarely spirally striated, umbilicate or not. The umbilicus, when present, often partially or entirely filled with callus. Aperture semi-circular or oval. Outer lip sharp; inner lip thickened by a callus. Excessively abundant from the Trias onward.

Fig. 896.

Natica (*Amauropsis*) *Willemeti*, Lam. Calcaire Grossier; Damery, near Epernay.

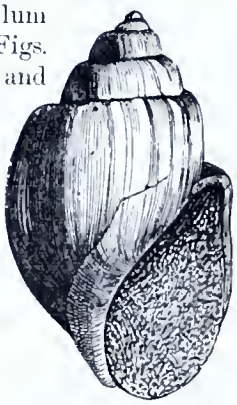


Fig. 897.

Natica (*Amauropsis*) *bulbiformis*, Sowb. Upper Cretaceous; St. Gilgen on Wolfgangsee, Austria.

Fig. 898.

Deshayesia cochlearia, Brongt. sp. Oligocene; Monte Grumi, near Vicenza.

Sub-genera: *Ampullina*, Lam. (Fig. 895); *Amauropsis*, Mörch (Figs. 896, 897); *Amaura*, Möll.; *Lunatia*, *Cernina*, Gray; *Neverita*, Risso; *Mamilla*, Schum., etc.

Deshayesia, Raul. (Fig. 898). Like *Natica*, but inner lip with thick callus and denticulated. Miocene and Pliocene.

Family 6. **Xenophoridae.** Deshayes.

Shell turbinate, without nacreous layer; whorls flat, often covered with agglutinated foreign bodies. Base conical or flat, with a sharp peripheral keel. Aperture obliquely quadrilateral. Operculum horny. Silurian to Recent.

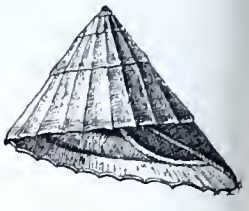


Fig. 899.

Xenophora heliacus, d'Orb. sp. Upper Lias; La Verpillière, near Lyons.

The *Xenophoridae* are an ancient family, the modern representatives of which have acquired a high differentiation. The radula is like that of the *Capulidae*, *Littorinidae*, and *Strombidae*, not like that of the *Trochidae*. The earlier forms, encountered in the Silurian, present a great superficial resemblance to the Palaeozoic *Trochus* species.

Eotrochus, Whitf. (Fig. 899). Thin-shelled, turbinate, widely umbilicate. Whorls flat, rarely with agglutinated foreign particles. Base concave, its periphery formed by a compressed lamellar belt. Silurian to Recent.

Omphalopterus, Roem. Depressed turbinate, widely umbilicate. The wide peripheral margin at the base composed of two lamellae, separated by a slit. Silurian.

Clisospira, Billings; *Autodetus*, Lindström. Silurian.

Xenophora, Fischer (*Phorus*, Montf.), (Fig. 900). Low trochiform, narrowly umbilicate. Whorls usually covered above with agglutinated extraneous objects. Cretaceous to Recent.

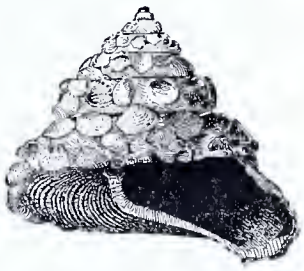


Fig. 900.

Xenophora agglutinans, Lam. Calcaire Grossier Damery, near Epernay.

Family 7. **Ampullariidae.** Gray.

This family inhabits fresh or brackish water, and is found in Africa, Asia, and tropical America. Some of their shells are hardly to be distinguished from *Natica*. The animal possesses a lung cavity above the right gill. Fossil forms occur in freshwater deposits of Cretaceous age at Rognac, near Marseilles, and also in the early Tertiary.

Family 8. **Valvatidae.** Gray.

Shell composed of few whorls, conical or discoidal, umbilicate. Aperture round, with continuous peristome. Operculum horny, circular, multispiral. Upper Jura to Recent.

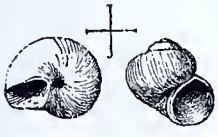


Fig. 901.

Valvata piscinalis, Müll. Upper Miocene; Vargas, Transylvania.

The genus *Valvata*, Müll. (Fig. 901), is small, and varies from turbinate to discoidal. It comprises about twenty-five recent species, inhabiting the fresh waters of Europe and North America. It is initiated in the Purbeck, but does not become at all abundant until the Tertiary.

Family 9. **Viviparidae.** Gill.

Shell conical or turbinate, with thick epidermis; imperforate or with narrow umbilicus. Whorls smooth, tubular or angular. Aperture rounded, oval, sub-angular posteriorly, with continuous peristome. Operculum horny, concentrically striated, with eccentric nucleus. Jura to Recent.

Viviparus, Montf. (*Paludina*, Lam.), (Fig. 902). This, the principal genus, is abundant in fresh water of all parts of the globe, with the exception of tropical and South America. Several other genera and subgenera are recognised, such as *Campeloma*, Raf. (*Melantho*, auct.), of North America, comprising mostly smooth, thick-shelled species, with thickened inner lip; *Tulotoma*, Haldem., including forms with angular whorls, North America; *Margarya*, Nev., China; *Lioplax*, Troschel; *Laguncula*, Benson; *Tylopoma*, *Boskovicia*, Brusina, etc.

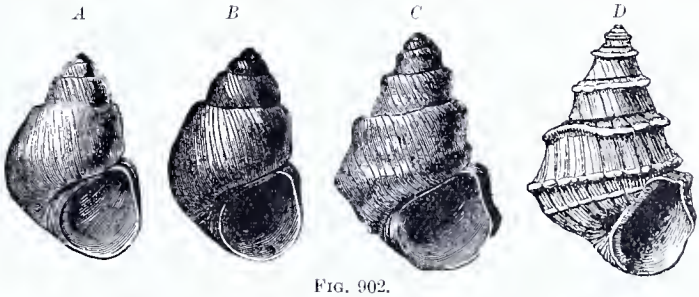


Fig. 902.

A, *B*, *Viviparus Brusinae*, Neumayr. *C*, *V.* (*Tulotoma*) *Forbesi*, Neumayr. Pliocene; Isle of Cos. *D*, *V.* (*Tulotoma*) *Hoernesi*, Neumayr. Pliocene; Novska, Slavonia.

Typical species of this genus are found in the Wealden clays. Vast numbers of *Viviparus* occur in the Pliocene of Southern Hungary, Croatia, Slavonia, Roumania,

and the Island of Cos, where they are remarkable for their extreme variability. Neumayr has described a number of mutation series from this horizon, which begin with smooth *Viviparus* species, and terminate with angular *Tulotoma*-like forms.

Family 10. **Amnicolidae.** Tryon.

Shell turbinate to turreted, small, usually thin, and either smooth, longitudinally ribbed, or spirally keeled. Aperture ovate; operculum horny or calcareous, spiral or concentric. Cretaceous to Recent.

These are fresh or brackish water inhabitants, some of which, however, are able to survive for a considerable period on land. It is difficult to distinguish the different genera belonging to this family by means of shell characters alone. All the forms are diminutive.

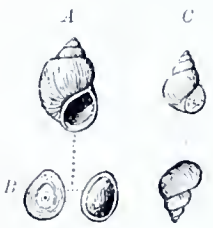


Fig. 903.

A, *Bythinia tentaculata*, Linn. sp. Upper Miocene; Miocic, Dalmatia. *B*, Operculum of same. *C*, *B. gracilis*, Sandb. Fresh-water Molasse; Oberkirchberg, near Ulm.

Bythinia, Leach (Fig. 903). Thin-shelled, turbinate, with umbilical fissure. Peristome continuous, outer lip sharp. Operculum calcareous, concentric. Wealden to Recent.

Fig. 904.

Nematura pupa, Nyst. sp. Oligocene; Hackenheim, near Alzey.

Fig. 905.

Nystia Chastelii, Nyst. sp. Middle Oligocene; Klein-Spouwen, Belgium.

Fig. 906.

Hydrobia (*Litorinella*) *acuta*, A. Braun. Miocene; Weissenau, near Mayence.

Staliola, Brusina. Outer lip thickened; operculum calcareous. Cretaceous to Miocene.

Fossarulus, Neumayr. Like the last, but with spiral ribs. Upper Miocene.

Nematura, Benson (*Stenothyra*, Benson), (Fig. 904). Like *Bythinia*, but aperture contracted. Operculum calcareous, spiral. Tertiary and Recent.

Nystia, Tourn. (*Forbesia*, Nyst.), (Fig. 905). Outer lip reflected; operculum calcareous, spiral. Tertiary and Recent.

Assiminea, Leach. Tertiary and Recent.

Hydrobia, Hartm. (*Littorinella*, Braun; *Tournoueria*, Brusina), (Fig. 906). Conical to turreted, acuminate, smooth. Aperture oval; operculum horny, paucispiral. Cretaceous to Recent. The Indusia Limestone (Lower Miocene) of Auvergne is almost exclusively composed of the shells of *H. Dubuissoni*, Bouill. Similarly, the Littorinella Limestone of the Main Basin which is of equivalent age, is made up of the shells of *H. acuta*, Braun. Strata in the fresh-water limestone of Nördlingen are charged with *H. trochulus*, Sandb.; and the Upper Eocene marl of St. Ouen is filled with the remains of *H. pusilla*, Prév. sp.

Other genera and sub-genera closely related to the foregoing are *Bythinella*, Moq.; *Amnicola*, Gould; *Belgrandia*, *Lartetia*, Bourguignat; *Lapparentia*, Berthelin.

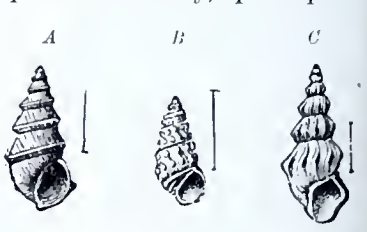


Fig. 907.

A, *Pyrgula Eugeniae*, Neumayr. Upper Miocene; Arpatak, Transylvania. *B*, *Micromelania* (*Diana*) *Haueri*, Neumayr. sp. Upper Miocene; Miocic, Dalmatia. *C*, *Mohrensternia inflata*, Andrzewsky. Congerien Stage (Miocene); Inzersdorf, near Vienna.

Pyrgula, Christofori and Jan. (Fig. 907, *A*). Turreted, whorls spirally keeled or ribbed. Peristome continuous. Tertiary and Recent.

Genera allied to the last are *Micromelania*, Brus. (Fig. 907, *B*); *Mohrensternia*, Stol. (Fig. 907, *C*); *Pyrgidium*, Tournouer; *Prososthenia*, Neumayr. Tertiary.

Lithoglyphus, Ziegl. (Fig. 908). Globose or ovate, with short spire; rather thick and solid. Aperture large, obliquely oval; inner lip thickened. Tertiary and Recent; Europe. Similar forms, *Somatogyrus*, Gill, and *Flumincola*, Stimpson, occur in North America. There are other related genera in South-Eastern Asia and South America.

Fig. 908.

Lithoglyphus fuscus, Ziegler. Upper Miocene; Malino, West Slavonia.

Family 11. **Rissoidae**. Troschel.

Shell small, thick, turbinate to turreted, usually ribbed or spirally striated, rarely smooth. Aperture oval, angular posteriorly, often with anterior canal. Operculum horny, paucispiral. Jura to Recent.

Rissoina, d'Orb. (Fig. 909). Turreted, transversely ribbed, rarely smooth; outer lip arcuate, generally thickened; aperture somewhat notched or effuse at the base. Dogger to Recent; mainly Tertiary.

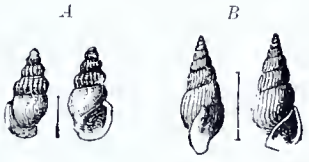


Fig. 909.

A, *Rissoina amoena*, Zitt. Tithonian; Stramberg, Moravia. *B*, *R. decussata*, Montf. Miocene; Steinabrunn, near Vienna.

Fig. 910.

A, *Rissoa turbinata*, Lam. sp. Oligocene; Weinheim, near Alzey. *B*, *R.* (*Alvania*) *Montagui*, Payr. Miocene; Steinabrunn, near Vienna.

Rissoa, Frém. (Fig. 910). Turreted, transversely ribbed or cancellated, aperture entire below. Jura to Recent.

Family 12. **Turritellidae**. Gray.

Shell turreted, with high acuminate spire. Whorls numerous, usually spirally ribbed or striated. Aperture oval, round or quadrangular, sometimes with faint anterior canal. Outer lip thin, peristome discontinuous. Operculum horny, multispiral. Marine. Trias to Recent.

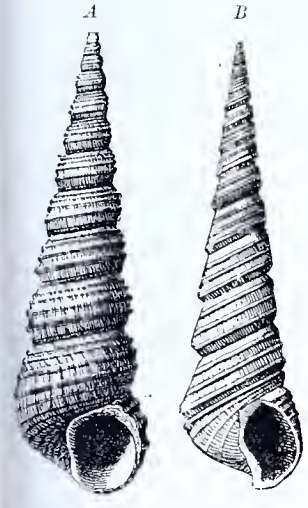


Fig. 911.

A, *Turritella turris*, Bast. (*T. terebra*, Ziet. non Linn.). Miocene Molasse; Ermingen, near Ulm. *B*, *T. imbricataria*, Lam. Calcaire Grossier; Grignon, near Paris.

Turritella, Lam. (Figs. 911, 912). Spire very high; aperture oval or rounded quadrilateral; outer lip thin, excavated behind, and slightly produced in front. Trias to Recent; maximum in Tertiary. The older Mesozoic species are usually small.

Fig. 912.

Turritella (*Mesalia*) *multisulcata*, Lam. Eocene; Calcaire Grossier; Grignon, near Paris.

Fig. 913.

Glauconia Kefersteini, Goldf. Middle Cretaceous; Dreistätten, near Wiener-Neust.

Sub-genera: *Mesalia*, Gray (Fig. 912). Like the last, but aperture with shallow canal, and twisted inner lip. Tertiary to Recent.

Protoma, Baird (*Proto*, p.p. Defr.). Aperture oval, anteriorly with canal-like contraction, which is surrounded externally by a thick swelling. Tertiary and Recent. *P. cathedralis*, Brgt.

Glauconia, Giebel (*Omphalia*, Zekeli; *Cassiope*, Coq.), (Fig. 913). Thick-shelled, conical to turreted, narrowly umbilicate. Whorls spirally ribbed, rarely smooth.

Aperture oval, with faint canal; outer lip with anterior and median emargination. Abundant in the Cretaceous.

Family 13. **Vermetidae.** Adams.

Shell tubular, the earlier whorls spiral, the later ones irregularly twisted, free or attached. Aperture round; operculum horny, sometimes wanting. Carboniferous to Recent.

Some fossil *Vermetidae* are liable to be mistaken for *Serpulidae*, but differ from them nevertheless in the structure of the shell and spiral nucleus. The determination of the few Palaeozoic and Mesozoic forms is uncertain.

Vermetus, Adans. (Figs. 914, 915). Shell usually attached, irregularly tubular, internally vitreous, and often with septa. Carboniferous (?) to Recent. Abundant in the Tertiary.

Fig. 914.

Vermetus (*Thylacodes*) *arenarius*, Linn. Miocene: Grund, near Vienna. 1/2.

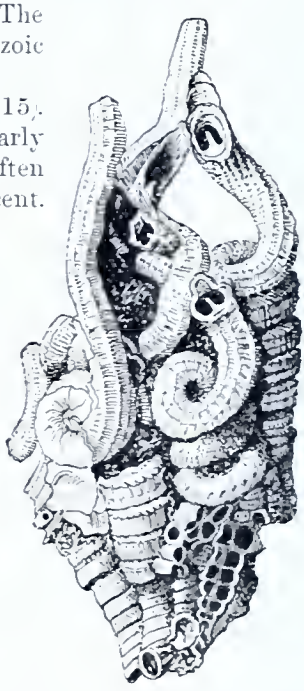


Fig. 915.

Petaloconchus intortus, Lam. Pliocene; Montespertoli, near Florence. Some of the tubes are fractured, and show the internal lamellae.

Fig. 916.

Siliquaria striata Desh. Calcaire Grossier; Chaussy, near Paris.

Sub-genera: *Thylacodes*, Guettard (Fig. 914); *Petaloconchus*, Lea (Fig. 915). Tertiary and Recent.

Siliquaria, Brug. (Fig. 916). Shell free, coiled in a loose spiral. Aperture lateral, and with a slit which continues as a fine cleft or row of pores throughout the entire length of the shell. Cretaceous to Recent.

Family 14. **Caecidae.** Adams.

Shell small, discoidal in early stages, later becoming tubular. The decollated nucleus replaced by a septum. Operculum round, horny. Tertiary and Recent.

Caecum, Flem. About one hundred Recent and twenty Tertiary species are known.

Family 15. **Melaniidae.** (Lamarck) Gray.

Shell turreted to oval, with thick, dark-coloured epidermis. Apex usually truncated and corroded. Aperture oval, sometimes canaliculate. Operculum horny, spiral. Jura to Recent.

Living species inhabit fresh, or more rarely brackish, waters of Southern Europe and the warmer zones of Africa, Asia, and America.

Melania, Lam. (Fig. 917). Shell smooth or spirally striated, or with transverse ribs or nodes. Aperture oval, anteriorly rounded. Upper Jura to Recent.

Fig. 917.

Melania Escheri, Brongt. Miocene; Michelsberg, near Ulm.

Stomatopsis, Stache. Whorls platform-like, with strong transverse ribs; aperture rounded, with entire, thickened, and reflected margins. Lowermost Eocene (Cosina Beds); Istria and Dalmatia.

Pyrgulifera, Meek (*Hautkenia*, Munier-Chalm.), (Fig. 918). Shell thick, elongate-oval, with platform-like, transversely ribbed, and spirally striated whorls. Aperture oval, sometimes with very faint canal. Upper Cretaceous of Europe and North America.

Paramelania, Smith. Resembles the preceding. Living in Lake Tanganyika.

Fascinella, Stache; *Coptostylus*, Sandb.; *Faunus*, Montf.; *Hemisinus*, Swainson. Upper Cretaceous, Eocene, and Recent.

Melanopsis, Fer. (Figs. 919-921). Shell oval to turreted, smooth or ornamented. Base of columella truncated; aperture with short canal; inner lip callous. Upper Cretaceous to Recent. Remarkably abundant in Miocene and Pliocene.

Pleurocera, Raf. (Fig. 922). Like *Melania*, but aperture with faint canal, and outer lip sinuous. Cretaceous to Recent; occurs only in North America.

Fig. 918.

Pyrgulifera Pichleri, Hoernes sp. Upper Cretaceous; Ajka, Hungary.

Fig. 919.

Melanopsis gallo-provincialis, Math. Uppermost Cretaceous; Martigues, near Marseilles.

Fig. 920.

Melanopsis Martiniana, Fer. Miocene; Nussdorf, near Vienna.

Fig. 921.

Melanopsis (*Canthidomus*) *acanthica*, Neumayr. Upper Miocene; Miocic, Dalmatia.

Fig. 922.

Pleurocera strombiformis, Schloth. sp. Wealden; Osterwald, Hannover.

Goniobasis, Lea; *Anculosa*, Say (*Leptoxis*, Raf.); *Ptychostylus*, Sandb. Wealden. The first two occur Tertiary and Recent in North America only.

Family 16. **Nerineidae.** Zittel.

Shell turreted, pyramidal, or ovate, perforate or imperforate. Aperture anteriorly with short canal or shallow notch. Columella and lips with strong folds, continuous throughout the entire length of the spire. Outer lip thin, posteriorly with fissure-like incision, which leaves a small slit-band immediately beneath the suture on all the whorls. Marine. Trias to Cretaceous.

Aptyxiella, Fisch. (*Aptyxis*, Zittel non Troschel). Turreted, very slender, imperforate. Aperture quadrangular; inner and outer lips without folds; columella somewhat thickened. Trias to Upper Jura.

Trochalia, Sharpe (*Cryptoplocus*, Pict. and Camp.), (Fig. 923). Turreted to

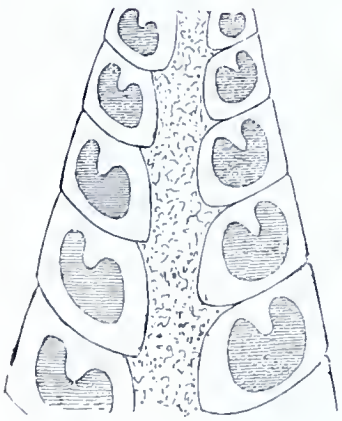


Fig. 923.

Trochalia consobrina, Zitt. Tithonian; Stramberg, Moravia. Longitudinal section.

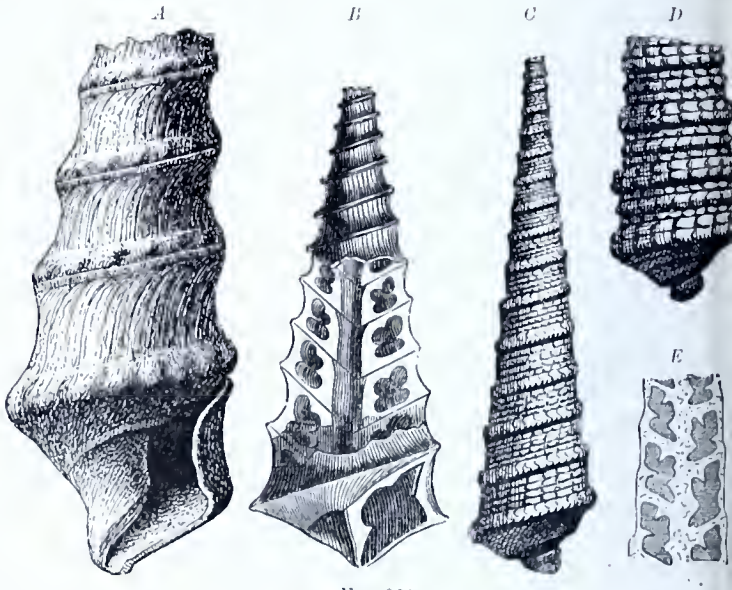


Fig. 924.

A, *Nerinea Defrancei*, d'Orb. Coral-Rag; Coulanges sur Yonne. *B*, *N. dilatata*, d'Orb. Coral-Rag; Oyonnax, Ain. *C-E*, *N. Hoheneggeri*, Peters. Tithonian; Stramberg, Moravia. *C*, 2/3. *D*, 1/1. *E*, Longitudinal section.

pyramidal, usually smooth and imperforate. The inner lip only has a strong, simple fold. Jura and Cretaceous.

Nerinella, Sharpe (*Pseudonerinea*, Loriol). Turreted, imperforate. Outer lip and sometimes also the columella with a simple fold. Jura.

Nerinea, Defr. (Fig. 924). Turreted or pyramidal, usually imperforate. Columella invariably, and inner and outer lips generally, with simple folds. Jura and Cretaceous; maximum in the Coral Rag (Upper Jura).

Ptygmatis, Sharpe (Fig. 925). Like the last, except that the folds on both lips and the columella are complicated by secondary constrictions and branchings. Jura and Cretaceous.

Itieria, Math. (Fig. 926). Elongate-oval, usually umbilicate. Spire short, sometimes insunken. Body whorl very large, more or less enveloping the preceding. Columella and both lips with folds. Jura and Cretaceous.

Fig. 925.

Ptygmatis pseudobruntrutana, Gemmellaro. Tithonian; Inwald, Carpathia. Vertical section.

Fig. 926.

Itieria Staszycii, Zeuschner. Tithonian; Inwald and Stramberg.

Family 17. **Cerithiidae.** Menke.

Shell turreted; aperture elongated, oval, or quadrilateral, anteriorly with short canal. Outer lip often thickened and reflected, or thin and sharp. Columella sometimes with one or two folds. Operculum horny, spiral. Marine and brackish water. Trias to Recent.

More than 1000 living, and about 500 fossil species are known, the latter being most numerous in the Eocene. The earliest forms are usually of small size, and have a nearly entire peristome.

Cerithinella, Gemm. (Fig. 927). Shell turreted, slender. Whorls numerous, flat, ornamented with spiral ribs or rows of small nodes. Aperture quadrilateral, with very faint canal. Jura.

Cryptaulax, Tate (*Pseudocerithium*, Cossmann). Small, turreted. Whorls with spiral ribs or rows of nodes and transverse folds. These last usually run continuously in a somewhat oblique direction from one whorl to the next. Aperture oval or quadrilateral, with scarcely perceptible canal. Trias and Jura.

Fig. 927.

Cerithinella armata, Goldf. Torulosus Beds (Middle Jura); Pretzfeld, Franconia.

Fig. 928.

Ceritella conica, Morris and Lyc. Great Oolite; Minchinhampton, England.

Ceritella, Morris and Lyc. (Fig. 928); Trias and Jura. *Fibula*, Piette (Fig. 929); Trias to Cretaceous. *Pseudalaria*, Huddlest.; *Ditretus*, Piette; Jura.

Fig. 929.

Fibula undulosa, Piette. Bathonian; Eparcy, Aisne.

Fig. 930.

Exelissa strangulata, d'Arch. sp. Bathonian; Eparcy, Aisne.

Fig. 931.

Bittium plicatum Brug. Oligocene; Ormoy, near Etampes, France.

Exelissa (Fig. 930). Very small, turreted; whorls with strong, continuous transverse ribs and spiral striae. Aperture contracted, rounded, without canal, sometimes slightly separated off, and with continuous peristome. Abundant in the Jura.

Bittium, Leach (Fig. 931). Turreted, with granulated spiral ribs, and numerous transverse costae. Aperture with short, straight canal; outer lip sharp. Jura to Recent. Abundant in the Tertiary.

Triforis, Deshayes; *Cerithiopsis*, Forbes. Tertiary and Recent.

Eustoma, Piette. Aperture with long canal, which is often closed, however, by margins of the inner and outer lip. Inner lip callous and strongly dilated; outer lip expanded. Jura.

Fig. 932.

Cerithium serratum, Brug. Calcaire Grossier; Damery, near Epernay.

Fig. 933.

Cerithium (*Vertagus*) *nudum*, Lam. Eocene; Chaumont, near Paris.

Fig. 934.

Potamides (*Tympanotomus*) *margaritaceum*, Brocchi. Oligocene; Hackenheim, near Alzey.

Fig. 935.

Potamides (*Lampania*) *pleurotomoides*, Desh. Middle Meeressand; Mortefontaine, Seine-et-Oise.

Cerithium, Brug. (Figs. 932, 933). Turreted, imperforate, without epidermis. Aperture oblong, ovate, with backwardly curved canal; outer lip often somewhat reflected. Columella concave, frequently with one or two folds. Certain Tertiary species attain a length of half a meter (*C. giganteum*). Jura to Recent; maximum in Eocene.

Sub-genera: *Vicarya*, d'Arch.; *Vertagus*, Klein (Fig. 933); *Bellardia*, Mayer, etc.

Potamides, Brongt. (Figs. 934, 935). Turreted, with epidermis; aperture with

emargination or faint canal. Inhabits only brackish water or estuaries. Cretaceous to Recent.

Sub-genera: *Tympanotomus*, Adams (Fig. 934); *Pyrazus*, *Telescopium*, Montf.; *Cerithidea*, Swains.; *Lampania* (Fig. 935); *Pyrenella*, Gray; *Sandbergia*, Bosq.

Family 18. **Aporrhaidae**. Philippi.

Shell fusiform, turreted, or conical ovate. Aperture produced anteriorly in a canal. Outer lip expanded in a wing-like or digitiform fashion, or thickened. Operculum horny. Marine. Jura to Recent; maximum in Jura and Cretaceous.

Alaria, Morris and Lyc. (Figs. 936-938). Shell turreted; aperture with long or short canal. Outer lip not overriding the last whorl, digitated or winged. Spire and body whorl often retaining traces of apertures at earlier stages. Very abundant in Jura and Cretaceous.

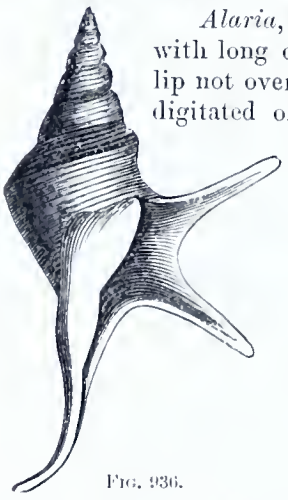


Fig. 936.

Alaria myurus, Deslongch. Lower Oolite; Bayeux, Calvados.

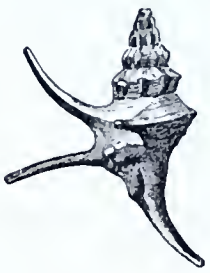


Fig. 937.

Aloria armata, Morris and Lye. Great Oolite; Minchinhampton, England.

Fig. 938.

Alaria (*Anchura*) *carinata*, Mant. Gault; Folkestone, England.

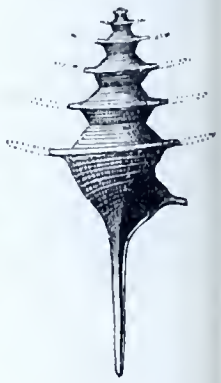


Fig. 939.

Spinigera semicarinata, Goldf. sp. Callovian; Montreuil-Bellay, Maine-et-Loire.

Sub-genera: *Dicroloma*, Gabb; *Anchura*, Conrad (Fig. 938). Jura and Cretaceous. *Diempterus*, Piette. Jura.

Spinigera, d'Orb. (Fig. 939). Whorls keeled and ornamented with two opposite rows of spines. Jura.

Aporrhais, da Costa (*Chenopus*, Phil.), (Figs. 940-942). Like *Alaria*, but margins of aperture elongated posteriorly in a canal, which remains either attached to the spire, or extends free from the same. Outer lip expanded, digitated, or lobed. Jura to Recent.

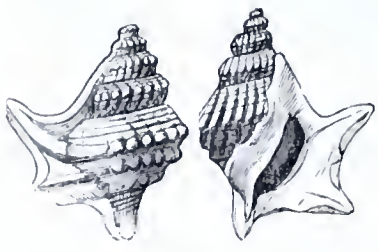


Fig. 940.

Aporrhais tridactylus, A. Braun. Oligocene; Hackenheim, near Creuznach.

Fig. 941.

Aporrhais (*Dimorphosoma*) *calcarata*, Sowb. Upper Greensand; Blackdown, England.

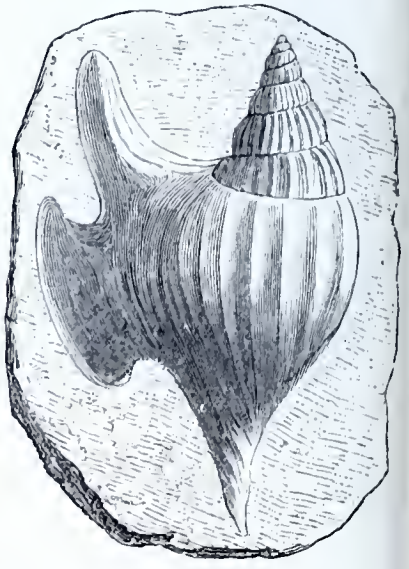


Fig. 942.

Aporrhais (*Lispodesthes*) *Reussi*, Geinitz var. *megaloptera*, Reuss. Plänер; Postelberg, Bohemia.

Sub-genera: *Alipes*, Conrad; *Arrhoges*, *Tessarolax*, *Helicaulax*, Gabb; *Ceratosiphon*, Gill; *Cuphoselenus*, *Malaptera*, Piette; *Pterocerella*, Meek; *Dimorphosoma*, St. Gardner (Fig. 941); *Lispodesthes*, White (Fig. 942). Jura and Cretaceous.

Family 19. **Strombidae.** d'Orbigny.

Shell conical, turreted, or fusiform, with acuminate spire. Aperture canaliculate; outer lip often expanded, anteriorly with an emargination. Operculum horny. Jura to Recent.

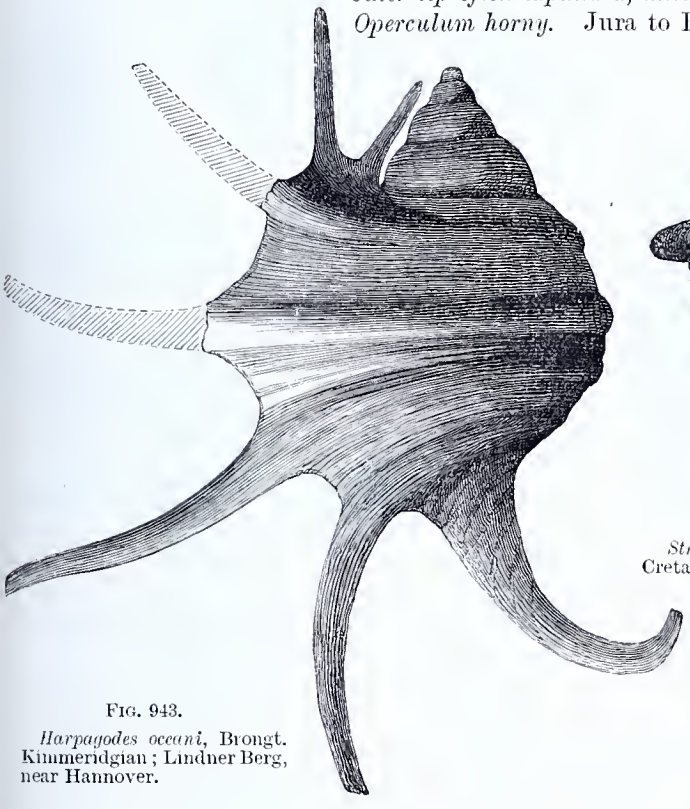


Fig. 943.

Harpagodes oceani, Brongt. Kimmeridgian; Lindner Berg, near Hannover.

Fig. 944.

Strombus crassilabrum, Zitt. Gosau-Cretaceous; St. Gilgen, Austria.

Although the shells of this family are excessively variable, the animals themselves exhibit great uniformity of structure.

Harpagodes, Gill (Fig. 943). Spire short, body whorl very large. Canal long, reflected. Outer margin produced in a number of tubular spinous processes, the posteriormost of which rests against the spire and extends nearly to the apex. Jura and Cretaceous.

Pterocera, Lam. (*Heptadactylus*, Klein). Spire short; canal bent sideways. Outer margin wing-like, with tubular spinous processes, beneath the most anterior of which is a deep notch. Recent.

Pterodonta, d'Orb.; *Thersitea*, Coq.; *Pereiraea*, Crosse. Miocene.

Strombus, Linn. (*Oncoma*, Mayer), (Fig. 944). Shell ovoid, tuberculose or spinose, solid; spire with several whorls; body whorl very large. Aperture elongate, obliquely truncated and channelled anteriorly, canaliculate posteriorly. Outer margin dilated in wing-like fashion, usually thick, often produced behind, sinuate and sometimes channelled in front. Columellar border simple, enamelled. Cretaceous to Recent.

Pugnellus, Conrad; Cretaceous. *Struthiolaria*, Lam.; Tertiary and Recent.

Fig. 945.

Seraphs sopitum, Brander sp. Calcaire Grossier; Grignon.

Seraphs, Montf. (*Terebellum*, Lam.), (Fig. 945). Shell elongate, sub-cylindrical; spire short, summit obtuse. Body whorl very large, smooth or striated. Aperture longitudinal, narrow posteriorly, and slightly

dilated anteriorly; canal short. Outer margin thin, simple, obliquely truncated anteriorly, sometimes prolonged in the spire posteriorly by a callosity. Columellar border smooth, straight. Tertiary and Recent.

Rostellaria, Lam. Spire high, whorls smooth. Aperture produced anteriorly in a beak-like canal, and continued posteriorly as a narrow channel resting on the spire. Outer margin with denticulate processes, notched anteriorly. Late Tertiary and Recent.

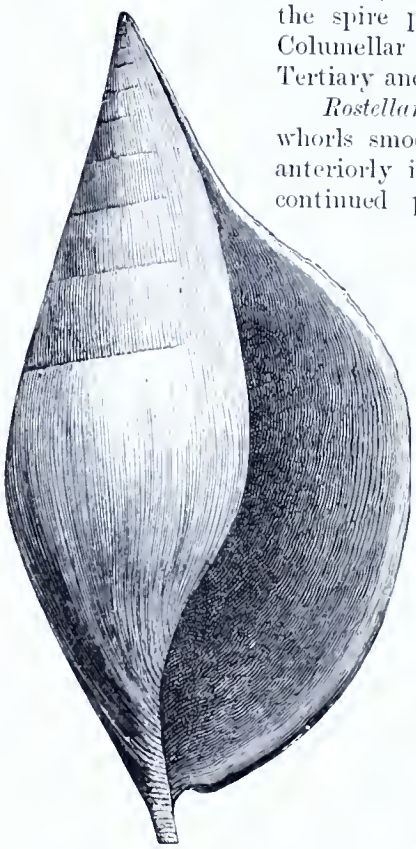


Fig. 946.

Hippochrenes Murchisoni, Desh. Calcaire Grossier; Damery, near Epernay.

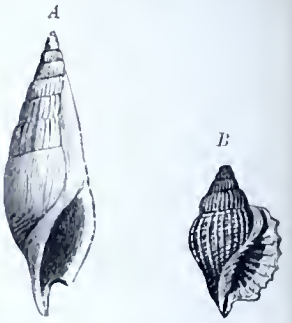


Fig. 947.

A, *Rimella fissurella*, Lam. Calcaire Grossier; Damery, near Epernay. *B*, *R. Bartonensis*, Sowb. sp. Calcaire Grossier; Grignon.

Hippochrenes, Montf. (*Orthaulax*, *Cyclolomops*, Gabb), (Fig. 946). Like the last, but outer margin expanded in wing-like fashion, and destitute of processes. Upper Cretaceous and Eocene.

Rimella, Agassiz (*Isopleura*, Meek), (Fig. 947). Surface cancellated. Outer lip with thickened margin, entire or crenulated. Upper Cretaceous to Recent.

Family 20. **Columbellariidae.** Fischer.

Shell thick, elongated oval, with short conical spire, and large, spirally ribbed, frequently cancellated body whorl. Aperture narrow, anteriorly with short canal, and posteriorly with a canal directed obliquely outwards. Inner lip callous, outer lip often thickened, denticulated, or somewhat reflected outwardly. Jura and Cretaceous.

Columbellaria, Rolle (Fig. 948). Surface covered with numerous spiral ribs, sometimes cancellated. Aperture long and narrow, broadening somewhat anteriorly. Outer lip denticulated internally, not thickened, somewhat reflected. Anterior and posterior canals short. Upper Jura.

Fig. 948.

Columbellaria coralina, Quenst. sp. Coral-Rag; Nattheim.

Fig. 949.

Zittelia crassissima, Zitt. sp. Tithonian; Stramberg.

Fig. 950.

Petersia costata, Gemm. Tithonian; Palermo.

Zittelia, Gemm. (Fig. 949). Like the last, but aperture very narrow or cleft-like. Outer lip much thickened in the middle. Tithonian.

Columbellina, d'Orb.; Cretaceous. *Petersia*, Gemm. (Fig. 950); Tithonian.

Family 21. **Cypraeidae.** Gray.

Shell ovate, convolute. Spire short, nearly or completely covered in the adult by the very large body whorl. Aperture of equal length with the shell, narrow, anteriorly and

posteriorly produced in a usually short canal. Outer lip inflected. Operculum wanting. Upper Jura to Recent.

Recent *Cypraecidae*, of which about 210 species are known, inhabit principally the warmer seas. They are often remarkable for their beautiful coloration, and sometimes attain considerable size. Jurassic species are sparse; Tertiary ones rather more abundant.

Cypraea, Linn. (Fig. 951). Ovoid, ventricose, enamelled, smooth, lirate, or tuberculate; spire exposed or enveloped. Aperture narrow, extending the whole length of the shell, and canaliculate at each extremity. Inner lip and the inrolled outer lip generally crenulate. Jura (*C. titonica*, Stefani) to Recent.

Fig. 951.
Cypraea subexcisa, A. Braun. Oligocene; Weinheim, near Alzey.

Fig. 952.
Trivia affinis, Duj. sp. Miocene; Pontlevoy, Touraine.

Fig. 953.
Erato laevis, Don. Miocene; Niederleis, Austria.

Trivia, Gray (Fig. 952). Like the preceding, but smaller, and sculptured with raised transverse riblets. Anterior channel not prolonged, wide and slightly reverted. Tertiary and Recent.

Erato, Risso (Fig. 953). Small, ovoid or pyriform, with short conical spire. Aperture narrow. Inner lip smooth, except for anterior columellar folds; outer lip denticulate. Canal notch-like, broad. Cretaceous to Recent.

Family 22. **Ovulidae.**

Like the Cypracidae, except that the spire is convolute instead of produced and covered, and the marginal teeth of the radula are peculiarly modified. Tertiary and Recent.

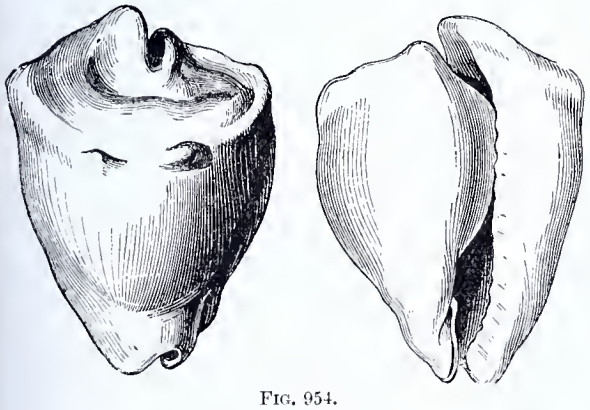


Fig. 954.
Gisortia tuberculosa, Duclos. Lower Eocene; Cuise-la-Mothe.

Ovula, Brug. Shell ovate or fusiform, the spire completely enveloped. Aperture produced anteriorly and posteriorly as a canal. Inner lip smooth; the outer inflected, smooth, or denticulated. Tertiary and Recent.

Gisortia, Jousseaume (Fig. 954). Large, thick-shelled, ovate, with short convolute spire. Surface typically keeled or coarsely tuberculate. Body whorl with a blunt ridge; aperture anteriorly and posteriorly with a short canal. Eocene. *G.* (*Strombus*) *gigantea*, Goldf. sp.

Pedicularia, Swainson. Miocene to Recent.

Family 23. **Cassididae.** Adams.

Shell thick, inflated, globularly ovate, sometimes varicose; spire short, body whorl very large. Aperture narrow, elongate, anteriorly with short canal. Inner lip resting on an extensive callus, sometimes granulated or wrinkled. Outer lip more or less thickened. Operculum horny, with marginal nucleus. Marine. Upper Cretaceous to Recent.

Cassidaria, Lam. (*Morio*, Montf.; *Galeodea*, Link.), (Fig. 955). Shell ventricose, not varicose. Canal long, twisted, reverted, or bent sidewise. Inner lip greatly expanded, outer lip reflected, often crenulate. Columellar border plicate. Upper Cretaceous to Recent; maximum in Eocene.

Fig. 955.

Cassidaria carinata, Lam. Calcaire Grossier; Grignon.

Fig. 956.

Cassidaria (*Sconsia*) *ambigua*, Solander sp. Oligocene; Lattorf, near Bernburg.

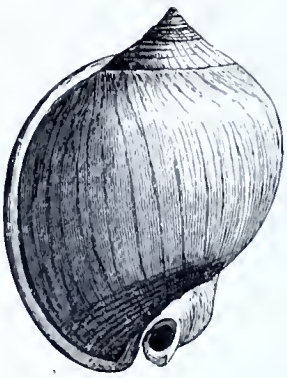


Fig. 957.

Cassis saburon, Lam. Miocene; Gainfahrn, near Vienna.

Sub-genus: *Sconsia*, Gray (Fig. 956). Last whorl with varix; canal short and straight. Upper Cretaceous to Recent.

Cassis, Lam. (Fig. 957). Shell ovoid, ventricose, having irregular varices. Spire short, aperture elongate. Outer lip thickened, reflected, usually denticulate in the interior. Inner lip callous, expanded, denticulate, wrinkled, or granulate. Canal very short, broad, sharply recurved, directed upward posteriorly. Tertiary and Recent.

Fig. 958.

Pyrula reticulata, Lam. sp. Miocene; Grund, near Vienna.

Family 24. **Doliidae.** Adams.

Shell thin, inflated. Spire very short, body whorl very large, longitudinally ribbed or cancellated. Aperture wide, oval; canal straight or curved. Operculum absent. Cretaceous to Recent.

Dolium, Lam. Spirally ribbed. Outer lip notched internally; canal short, obliquely directed. Cretaceous to Recent.

Pyrula, Lam. (*Ficula*, Swainson), (Fig. 958). Spirally ribbed, grooved, or cancellated. Aperture very wide; outer lip sharp; canal long, broad, straight. Lower Cretaceous to Recent; maximum in Tertiary.

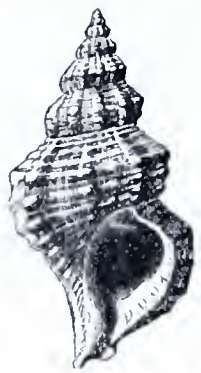


Fig. 959.

Tritonium (*Simpulum*) *flandricum*, de Kon. Oligocene; Weinheim, near Alzey.

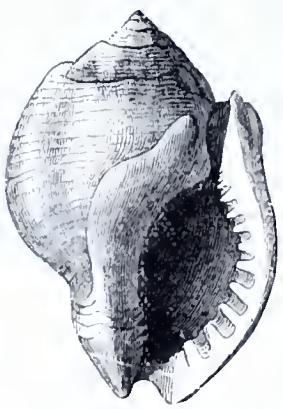


Fig. 960.

Ranella marginata, Brocchi, Miocene; Grund, near Vienna.

Family 25. **Tritonidae.** Adams.

Shell thick, ovate to fusiform, with epidermis. Spire moderately high, whorls varicose. Aperture with thickened outer lip, and open, straight, or slightly bent canal. Operculum horny, with marginal nucleus. Cretaceous to Recent.

Tritonium, Link. (*Triton*, *Lotorium*, Montf.), (Fig. 959). Spire elongated. The varices do not run continuously over more than a few whorls. Columella and inner lip callous or granulated. Outer lip thickened internally and notched. Cretaceous to Recent; abundant in the Tertiary.

Distortrix, Link. (*Persona*, Montf.). Tertiary and Recent.

Ranella, Lam. (Fig. 960). Like *Tritonium*, but with two opposite varices, which are continuous over all the whorls. Tertiary and Recent.

Superfamily 4. RACHIGLOSSA. Gray.

Radula reduced to three teeth or to one tooth in a transverse series.

These are carnivorous marine forms, which have their initiation in the Mesozoic, become somewhat numerous in the Cretaceous, and form an important element of the Tertiary and Recent faunas.

Family 1. Columbellidae. Troschel.

Shell small, ovate to fusiform, covered with epidermis, imperforate. Aperture narrow, canal short. Outer lip dentieulated internally, thiekened in the middle. Tertiary and Recent.

The typical genus, *Columbella*, Lamarck (Fig. 961), attains its maximum distribution in the Tertiary and Recent seas. It is divided into a number of sub-genera.

Fig. 961.

Columbella curta, Duj. Miocene; Lapugy, Transylvania.

Family 2. Buccinidae. Troschel.

Shell elongate-oval, covered with epidermis. Aperture wide, with short eanal. Outer lip sharp or thickened. Opereulum horny. Cretaceous to Recent.

Bucceinum, Linn. Inflated, smooth, or transversely ribbed. Spire moderately high; aperture wide; canal short, wide, open. Outer lip sharp and thin, inner lip somewhat callous. Distributed principally in waters of the more northerly zones (*B. undatum*, Linn.). Fossil in the Crag and Pleistocene.

Fig. 962.

Cominella cassidaria, A. Braun. Oligocene; Hackenheim, near Alzey.

Cominella, Gray (Fig. 962). Usually spirally ribbed. The last whorl somewhat depressed beneath the suture, so that the aperture forms a small groove posteriorly. Outer lip sharp or crenate internally. Upper Cretaceous to Recent.

Pseudoliva, Swains. (Fig. 963). Like the last, but outer lip with a small basal tooth or notch which corresponds to a groove on the body whorl. Upper Cretaceous to Recent.

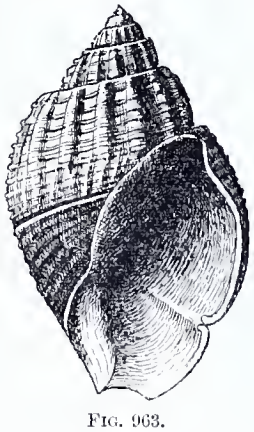


Fig. 963.

Pseudoliva Zitteli, Pethö. Upper Cretaceous; Fruska Gora, Hungary.

Fig. 964.

Pollia sublavata, Bast. sp. Miocene; Enzesfeld, near Vienna.

Pisania, Bivona (*Pisanella*, v. Koenen; *Taurinia*, Bellardi). Elongate-ovoid, spire moderately high. Whorls smooth or spirally striated. Outer margin thickened, notched internally. Tertiary and Recent.

Pollia, Gray (*Cantharus*, Bolten; *Tritonidea*, Swains.), (Fig. 964). Oval, inflated; spire and aperture of about equal length; surface usually spirally ribbed and transversely folded. Columella often with weak transverse folds; outer margin thickened, crenate internally. Aperture posteriorly with a short canal. Tertiary and Recent.

Phos, Montf. Shell elongate, buccinifform, turriculate; spire sharp, elevated, whorls ornamented with prominent longitudinal costae, and less salient spiral threads and sulci, often varicose. Aperture oblong; outer margin lirate within. Columella excavated, plicate in front; canal short, slightly twisted. Tertiary and Recent.

Fig. 965.

Eburna caronis, Brongt. sp. Eocene; Ronca, near Vicenza.

Fig. 966.

Nassa clathrata, Brocchi. Pliocene; Larniano, Tuscany.

Eburna, Lam. (*Dipsaccus*, Klein), (Fig. 965). Resembling *Nassa*, but smooth, perforated, and with deeply incised sutures; outer margin sharp. Tertiary and Recent.

Nassa, Martini (Fig. 966). Ovate, inflated. Aperture with short, reverted canal; inner lip callous, expanded; outer margin usually crenate internally. Sparse in Upper Cretaceous and Eocene, abundant in Miocene and Pliocene; living species exceeding 200 in number, and distributed in numerous sub-genera.

Cyclonassa, Agassiz; *Cyllene*, Gray; *Truncaria*, Adams; *Buccinopsis*, Deshayes. Tertiary and Recent.

Chrysodomus, Swains. (*Neptunea*, Bolten). Elongate-ovoid, inflated, sometimes sinistral, with rather short and sometimes bent canal. Cretaceous to Recent. *C. contrarius*, Lam. Crag.

Fig. 967.

Hemifusus subcarinatus, Lam. sp. Eocene (Sables moyens); Senlis, Seine et Oise.

Siphonalia, *Zemira*, *Metula*, Adams; *Euthria*, Gray; *Hemifusus*, Swainson (Fig. 967). Tertiary and Recent. *Mitraefusus*, *Genea*, Bellardi. Neocene.

Melongena, Schum. (*Pyrula*, Lam. p.p.; *Myristica*,

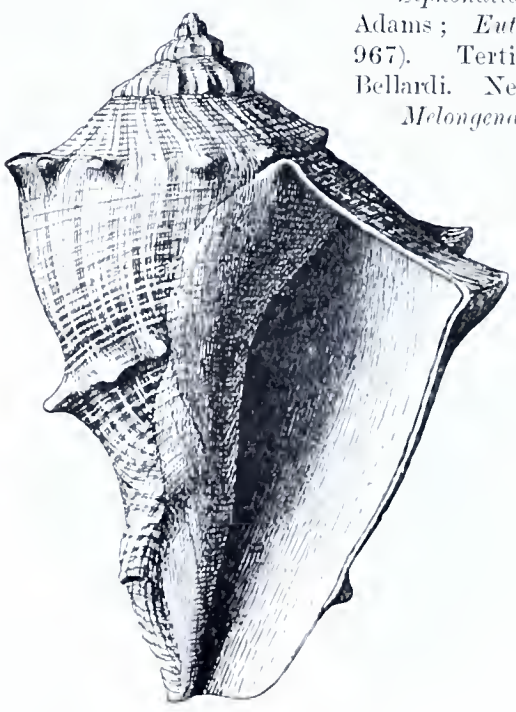


Fig. 968.

Melongena cornuta, Agassiz. Miocene; Bordeaux.

Fig. 969.

Tudicla rusticula, Bast. sp. Miocene; Grund, near Vienna.

Swains.), (Fig. 968). Pyriform, inflated, with short spire. Body whorl large,

longitudinally striated and beset with nodes or rows of spines. Inner lip smooth; aperture gradually becoming merged into the short and wide canal. Tertiary and Recent.

Fulgur, Montfort (*Busycon*, Bolten). Tertiary and Recent.

Tudicla, Bolten (Fig. 969). Resembles *Fulgur*, but has a straight and very long canal; inner lip with a fold. Cretaceous to Recent.

Strepsidura, Swains. (Fig. 970). Spire short; body whorl inflated, transversely ribbed; canal curved. Eocene and Miocene.

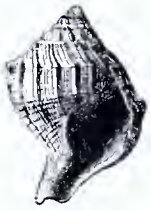


Fig. 970.

Strepsidura ficulnea, Lam. Calcaire Grossier; Damery, near Epernay.

Family 3. **Muricidae**. Tryon.

Shell thick. Spire moderately high; whorls with transverse swellings, ribs, or folia, and frequently spinose. Aperture rounded or oval; canal more or less elongated, wholly or partially covered by margins of the inner and outer lips. Operculum horny. Cretaceous to Recent.

Murex, Linn. (Figs. 971-973). Shell rounded, spire prominent. Surface with at least three, often more than three varices or transverse rows of spines or nodes on each whorl. Aperture ovate; inner lip smooth, outer lip thickened. Canal much prolonged, partially closed, usually spinose. Cretaceous to Recent.

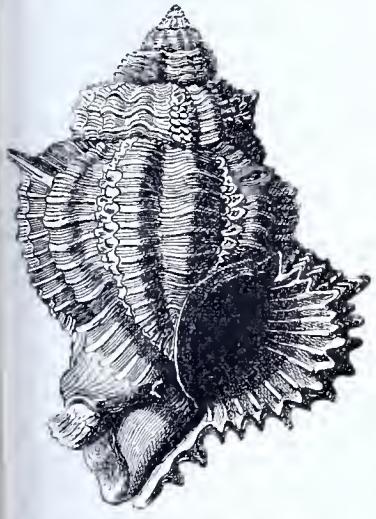


Fig. 971.

Murex (*Phyllonotus*) *Sedgwicki*, Micht. Miocene; Gainfahrn, near Vienna.

Fig. 972.

Murex spinicosta, Bronn. Miocene; Baden, near Vienna.

Fig. 973.

Murex (*Pteronotus*) *tricarinatus*, Lam. Eocene; Damery, near Epernay.

Fig. 974.

Typhis tubifer, Montf. Calcaire Grossier; Grignon, near Paris.

Sub-genera: *Haustellum*, Klein; *Rhinacantha*, Adams; *Chicoreus*, *Phyllonotus* (Fig. 971), Montfort; *Pteronotus*, Swainson (*Triplex*, Perry), (Fig. 973); *Oeinebra*, Leach, etc.

Typhis, Montf. (Fig. 974). Like *Murex*, but with hollow spines. Canal short, completely closed. Upper Cretaceous to Recent.

Trophon, Montf. Spire high. Longitudinal ribs replaced by thin lamellae. Canal open, somewhat curved. Tertiary and Recent.

Family 4. **Purpuridae**. Gray.

Shell thick, usually ovoid; spire short, body whorl large. Aperture wide, inner lip and columella more or less flattened; canal short. Operculum horny. Cretaceous to Recent.

Purpura, Brug. (Fig. 975). Imperforate; body whorl with transverse ribs or nodes. Aperture oval, columella flattened, smooth. Tertiary and Recent.

Rapana, Schum. (Fig. 976). Like the preceding, but perforate. Inner lip callous, expanded. Cretaceous to Recent.

Lysis, Gabb; *Stenomphalus*, Sandberger. Cretaceous and Tertiary.

Sistrum, Montf. (*Ricinula*, Lam.); *Monoceros*, Lam.; *Concholepas*, Lam.; *Cymia*, Mörch, etc. Tertiary and Recent.

Fig. 975.

Purpura exilis, Partsch. Miocene; Möllersdorf, near Vienna.

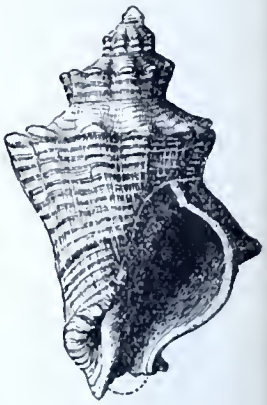


Fig. 976.

Rapana laxecarinata, Micht. Oligocene; Santa Ginstina, Italy.

Family 5. **Fusidae.** Tryon.

Shell turreted, fusiform or ovoid, generally without varices. Canal more or less elongated. Inner lip smooth, or with weak columellar folds; outer margin thin. Operculum horny. Jura to Recent.

These shells are sparse in the Upper Jura and Cretaceous, but abundant in the Tertiary and Recent. The animal differs but little from that of the *Buccinidae* and *Muricidae*.

Fusus, Lam. (*Colus*, Humph.), (Fig. 977). Shell narrow, elongate; spire acuminate. Aperture ovate; canal very long, straight, open. Outer margin thin, sometimes crenulate, and often striate within; columella smooth. Rare in Upper Jura and Cretaceous, very profuse in Tertiary and Recent.

Fig. 977.

Fusus longirostris, Brocchi. Miocene; Baden, near Vienna.

Fig. 978.

Clavella longaevus, Lam. Eocene; Damery, near Epernay.

Clavella, Swains. (*Cyrtulus*, Hinds), (Fig. 978). Thick-shelled, smooth, or with fine spiral striae. Body whorl suddenly contracted anteriorly. Canal very long, straight. Common in Eocene; rare Neocene and Recent.

Fig. 979.

Sycum bulbiformis, Lam. Calcaire Grossier; Grignon, near Paris.

Sycum, Bayle (*Leiostoma*, Swains.), (Fig. 979). Spire short; body whorl inflated, smooth, somewhat flattened below the suture. Inner lip smooth; canal straight. Common in the Eocene; rare in Miocene.

Fasciolaria, Lam. (Fig. 980). Like *Fusus*, but distinguished in general by having a shorter spire, more inflated body whorl, a wider and more sinuous or flexuous canal, and in that the anterior portion of the columella has two or three oblique plications. Cretaceous to Recent.

Latirus, Montf. (Fig. 981). Shell fusiform, turreted; spire costate. Aperture

oblong, outer margin relatively thin, crenulate; columellar border slightly twisted, with two or three small oblique plaits anteriorly; sometimes umbilicate. Cretaceous to Recent.

Pisanella, v. Koenen. Oligocene. *Peristernia*, Mörch; *Leucozonia*, Gray. Tertiary and Recent.

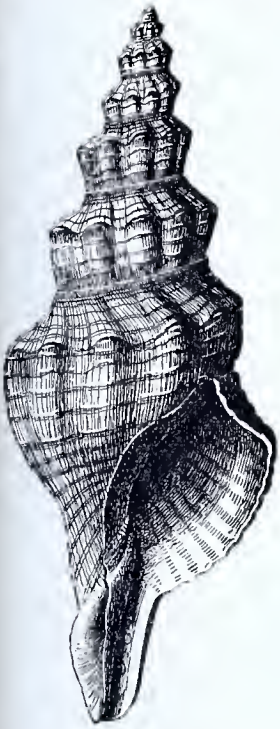


Fig. 980.

Fasciolaria Tarbelliana, Grat. Miocene; Grund, near Vienna.

Fig. 981.

Latirus cracticulatus, d'Orb. sp. Miocene; Lapugy, Transylvania.

Family 6. **Turbinellidae.**

Shell similar to those of the preceding family, but with strong, horizontal columellar folds. Tertiary and Recent.

Turbinella, Lam. (*Mazza*, Adams; *Mazzalina*, Conrad). Thick-shelled, ovate-conical, smooth; spire short and blunt, body whorl large; canal straight, elongated. Eocene to Recent.

Family 7. **Volutidae.** Gray.

Shell thick, ovate to fusiform, dull or lustrous. Spire short or long, body whorl large. Aperture elongated, with a short canal or notch; inner lip with columellar folds. Operculum usually absent. Cretaceous to Recent.

Fig. 982.

Marginella crassula, Desh. Calcaire Grossier; Chaumont, near Paris. 2/1.

This family, as here defined, contains genera distributed by malacologists amongst several families — *Marginellidae*, *Mitridae*, and *Volutidae*—all of which are characterised by the strong development of columellar folds; but it is likely that this structure originated independently in several phyla at intervals remote from one another. The initiation of well-marked genera with Volutoid plaits occurred in the Cretaceous. Subsequently their number increased, and a great many generic types became differentiated. The phylogeny of Tertiary and Recent forms has been ably worked out by Dall.[1]

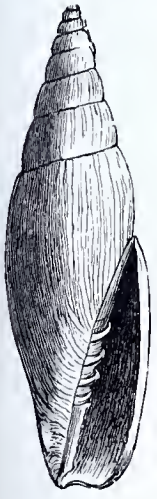


Fig. 983.

Mitra fusiformis, Brocchi. Pliocene; Rhodes.

Marginella, Lam. (Fig. 982). Shell oval or oblong, smooth, glistening. Spire short; aperture narrow, slightly canaliculate anteriorly. Columella with three or four oblique folds of about equal size; outer margin frequently thickened and dentate. Tertiary and Recent.

Mitra, Lam. (Fig. 983). Fusiform to elongate-oval, solid; spire high, acuminate; aperture narrow, channelled anteriorly. Columella with numerous oblique folds, the posterior plaits being often the strongest. Outer margin commonly thickened, and smooth internally. Abundant in the Tertiary and Recent.

Turricula (Klein), Adams. Like the last, but shell transversely ribbed. Cretaceous to Recent.

[1] Bull. Museum Comp. Zoology, vol. XVIII., 1889; Proc. U.S. Nat. Museum, vol. XII., 1890; Trans. Wagner Free Inst. Sci. Philad., vol. III., 1890.

Strigatella, Swains. (Fig. 984); *Cylindromitra*, Fischer (*Cylindra*, Schum.); *Imbricaria*, Schum.; *Volutomitra*, Gray. Tertiary and Recent.

Lyria, Gray (Fig. 985). Elongate-oval, transversely ribbed. Aperture narrow. Columella anteriorly with two much compressed and very large plications, behind (above) which are numerous weaker ones. Outer margin thickened. Tertiary and Recent.

Fig. 984.

Strigatella labratula, Lam. sp. Eocene; Grignon.

Fig. 985.

Lyria modesta, A. Braun. Oligocene; Weinheim.

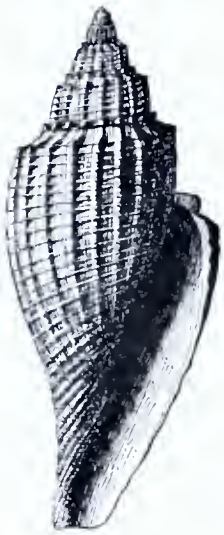


Fig. 986.

Volutilithes bicorona, Lam.? Eocene; Courtagnon, near Epernay.

Halia, Risso (*Priamus*, Beck). No columellar folds. Pliocene and Recent.

Volutilithes, Swains. (Fig. 986). Shell fusiform, spire elongate-conical; nucleus small, rising to a more or less acute apex. Whorls costate, typically spinose. Aperture anteriorly with short broad canal; columellar folds variable, several in number, those toward the anterior being generally the most pronounced. Abundant in the Cretaceous, Eocene, and Oligocene; only one recent species.

Allied genera and sub-genera: *Gosavia*, Stol.; *Leioderma*, *Rostellites*, Conrad; *Volutoderma* (Fig. 987), *Volutomorpha*, Gabb. Cretaceous.

Athleta, Conrad. Spire short, body whorl inflated, posteriorly with a row of spinous nodes. Inner lip callous, much expanded; columella anteriorly with three strong transverse folds, behind (above) which follow a few weaker ones. Outer margin thickened. Eocene and Miocene.

Voluta, Linn. (Fig. 988). Shell elongate-oval or fusiform, solid, broad, and with elevated, turbinate, smooth nucleus. Spire short, longitudinally plicate, the folds being elevated into obtuse tubercles on the base of the whorls. Aperture narrow, canaliculate behind and broad in front; inner margin often covered by a thin callus. Columella carrying many plaits, four or five of which are prominent, the remainder much smaller. Tertiary and Recent.

Sub-genera: *Fulgaria*, Schum.; *Scapha*, Gray (Fig. 988); *Volutella*, d'Orb.; *Aurinia*, Adams (*Volutifusus*, Conrad), etc.

Musica, Humphrey. Spire short, nucleus small. Aperture narrow, inner lip callous, with numerous transverse folds; outer margin thickened. Tertiary and Recent.

Cymbium, Klein (*Vetus*, Adams; *Melo*, Humph.). Cretaceous to Recent.

Fig. 987.

Volutilithes (*Volutoderma*) *elongata*, d'Orb. Gosau-Cretaceous; St. Gilgen, Austria.

Fig. 988.

Voluta (*Scapha*) *muricina*, Lam. Calcaire Grossier; Damery, near Epernay.

Family 8. **Harpidae.** Troschel.

Spire depressed; body whorl inflated, with sharp, uniformly spaced transverse ribs. Aperture wide, with short, broad canal. Inner lip callous. Operculum absent. Tertiary and Recent.

The typical genus *Harpa*, Lam. (*Silia*, Mayer), (Fig. 989), ranges from the Eocene to the present time.

? *Harpopsis*, Mayer (*Cryptoehorda*, Mörch), (Fig. 990). Elongate-oval; spire short, body whorl large, smooth, lustrous. Aperture with short recurved canal; inner lip callous. Common in the Eocene.

Fig. 989.

Harpa mutica, Lam. Calcaire Grossier; Grignon.

Fig. 990.

Harpopsis stromboides, Lam. sp. Calcaire Grossier; Damery, near Epernay.

Family 9. **Olividae.** d'Orbigny.

Shell elongate-oval to sub-cylindrical, solid, smooth, and glistening. Spire short; body whorl very large. Aperture narrow; outer lip sharp; columella anteriorly with an outwardly reflected callus. Canal very short. Cretaceous to Recent.

Oliva, Brug. (Fig. 991). Shell sub-cylindrical; suture line marked by a deep groove. Columellar callus obliquely folded. Cretaceous to Recent.

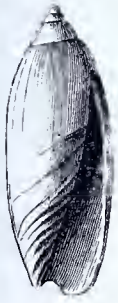


Fig. 991.

Oliva clavula, Lam. Miocene; Dax, near Bordeaux.

Fig. 992.

Aneilla glandiformis, Lam. Miocene; Steinabrunn.

Aneilla, Lam. (*Aneillaria*, Lam.), (Fig. 992). Shell oblong, occasionally acuminate. Suture usually covered over by a lustrous enamel-like callus. Aperture somewhat broadened anteriorly; columellar callus slightly twisted. Cretaceous to Recent.

Superfamily 5. TOXOGLOSSA. Troschel.

Radula typically with only two arrow-shaped teeth in each transverse row, although occasionally as many as five teeth are developed. Shell similar to that of the Raehiglossa.

This group is closely allied to the *Raehiglossa*, from which it probably became differentiated in the Cretaceous. The Tertiary and Recent species are excessively profuse. All are carnivorous and marine.

Fig. 994.

Terebra acuminata, Borson. Miocene; Baden, near Vienna.

Family 1. **Cancellariidae.** Adams.

Shell oval to turreted. Spire acuminate; body whorl inflated; surface transversely ribbed and in most cases cancellated. Aperture with short canal or notch; columella with several strong oblique folds, outer lip grooved internally. Upper Cretaceous to Recent.

The typical genus *Cancellaria* (Fig. 993) attains a maximum distribution in the late Tertiary and Recent.

Fig. 993.

Cancellaria cancellata, Linn. Miocene; Gainfahrn, near Vienna.

Family 2. **Terebridae.** Adams.

Shell turreted, slender, acuminate, with small body whorl. Aperture oval or quadrilateral; canal short, curved; outer lip sharp. Operculum horny. Tertiary and Recent.

Of the two leading genera, *Terebra*, Lam. (Fig. 994), and *Aeus*, Humphr., the first

is characterised by a line running parallel with the suture, and creating a narrow suture band.

Family 3. **Pleurotomidae.** Stoliczka.

Shell fusiform, with moderately high spire. Aperture elongated, produced anteriorly in a longer or shorter canal. Outer lip with a slit or notch below the suture. Operculum horny, sometimes absent. Cretaceous to Recent.

Upwards of 700 recent and 1000 fossil species have been described, of which 28 are Cretaceous.

Pleurotoma, Lam. (Figs. 995-998). Shell turriculated, spire long. Body whorl of nearly equal length with the spire; canal long and straight; columellar margin

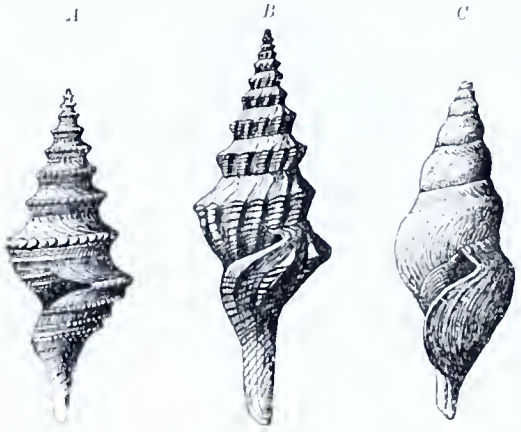


Fig. 995.

A, *Pleurotoma notata*, Brocchi var. (=*P. monilis*, Hoernes). Miocene; Baden, near Vienna. *B*, *P.* (*Surcula*) *Lamarcki*, Bell. Miocene; Baden, near Vienna. *C*, *P.* (*Surcula*) *belgica*, Nyst. Oligocene; Weinheim, near Alzey.

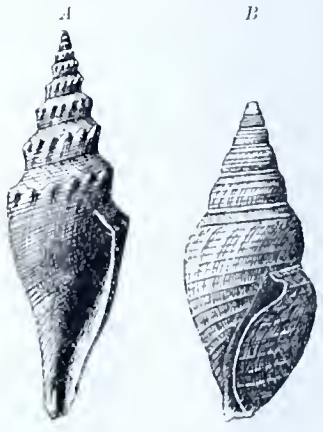


Fig. 996.

A, *Pleurotoma* (*Genota*) *ramosa*, Bast. Miocene; Grund, Hungary. *B*, *P.* (*Cryptoconus*) *filosa*, Lam. Calcaire Grossier; Grignon, near Paris.

smooth. Outer margin of the aperture with a narrow, deep sinus, situated at or some distance below the suture. Operculum pointed ovate, with apical nucleus. Cretaceous to Recent.

Sub-genera: *Surcula* (Figs. 995, *B*, *C*); *Genota*, Adams (Fig. 996, *A*); *Dolichotoma* (Fig. 997), *Oligotoma*, *Ronaltia*, Bellardi; *Cryptoconus*, v. Koenen (Fig. 996, *B*); *Drillia* (Fig. 998), *Bela*, Gray; *Lachesis*, Risso, etc.

Fig. 997.

Pleurotoma (*Dolichotoma*) *cataphracta*, Brocchi. Miocene; Baden, near Vienna.

Fig. 998.

Pleurotoma (*Drillia*) *incrassata*, Duj. Miocene; Steinabrunn, near Vienna. 2/1.

Fig. 999.

Clavatula asperulata, Lam. Miocene; Grund, Hungary.

Clavatula, Lam. (Fig. 999). Differs from *Pleurotoma* in that the outer margin is cut by a shallow triangular notch, and nucleus of operculum is situated in the middle of the anterior margin. Cretaceous to Recent. Sub-genera: *Pseudotoma*, *Clinura*, Bellardi.

Borsonia, Bellardi (Fig. 1000). Outer margin with a shallow notch; canal long and straight; columella with one or two folds; operculum unknown. Eocene to Recent.

Mangilia, Risso (Figs. 1001, 1002). Small, fusiform, imperforate, and typically with longitudinal costae or swellings. Aperture commonly narrow, with a short, truncated canal; inner margin varicose; sinus near the suture. Outer margin usually somewhat thickened, posteriorly with shallow notch. Tertiary and Recent.

Fig. 1000.

Borsonia Deluci, Nyst. Lower Oligocene; Lattdorf, near Bernburg.

Fig. 1001.

Mangilia angusta, Jan. Pliocene; Occiano, near Pisa.

Fig. 1002.

A, *Mangilia* (*Clathurella*) *strombillus*, Duj. Miocene; Kienberg, near Vienna. *B*, *M.* (*Homotoma*) *reticulata*, Brocchi. Pliocene; Sassuola, near Modena.

Fig. 1003.

Daphnella (*Raphitoma*) *vulpecula*, Brocchi. Pliocene; Sassuola, near Modena.

Allied genera are the following:—*Clathurella*, Carp. (Fig. 1002, *A*); *Homotoma* (Fig. 1002, *B*); *Atoma*, Bellardi; *Daphnella*, Hinds, with sub-genus *Raphitoma*, Bellardi (Fig. 1003); *Eucythara*, Fischer, etc.

Family 4. **Conidae.** Adams.

Shell convolute, turbinate, or sub-cylindrical, generally smooth. Spire short, conical or flattened. Aperture long, narrow, anteriorly notched. Outer lip sharp, sometimes with an anal sinus below the suture. Columella smooth. Operculum horny. Cretaceous to Recent.

This family is now enjoying its acme of development, having entered upon its ascendency during the Tertiary. The typical genus *Conus*, Linn. (Fig. 1004), is divided by malacologists into numerous sub-genera, connected with one another by intermediate forms. It is initiated in the Cretaceous.

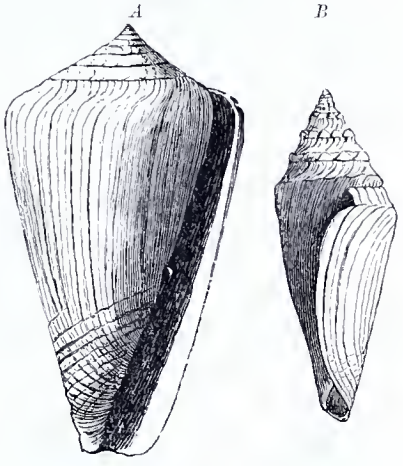


Fig. 1004.

A, *Conus ponderosus*, Brocchi. Miocene; Lapugy, Transylvania. *B*, *C. parisiensis*, Desh. Calcaire Grossier; Grignon, near Paris.

Conorbis, Swains. Characterised by a high spire, and a curved, outer lip, which is deeply notched posteriorly. Eocene and Oligocene.

Sub-Class 2. **EUTHYNEURA.** Spengel.

Gastropods in which the visceral nerve commissures are not crossed, but form a simple loop; the sexes are united (hermaphrodite); and the heart is often in front of the gill. Shell spiral or saucer-shaped, frequently vestigeal or absent; operculum generally wanting. Radula generally multiserial.

Order 1. OPISTHOBRANCHIA. Milne-Edwards.

Marine, water-breathing forms, either naked or shell-covered, in which the gills are placed behind the heart and lie free on the back or side; or true gills may be absent, being replaced by secondary or false gills. Heart with a single auricle.

The Opisthobranchiates, unlike the *Streptoneura* (Prosobranchiates), send the blood into the heart from behind, instead of from the anterior side. The gills, in the form of a more or less branched plume, lie on the right side, or are replaced by false gills not homologous with the ctenidium, arranged either in two rows on the back, or wreath-like around the anus. The gills are often covered by the mantle, and sometimes become completely atrophied. The radula generally resembles that of the Pulmonates. The body and nervous system usually exhibit bilateral symmetry.

Two sub-orders are recognised in the recent fauna: (1) *Nudibranchiata*, in which a shell is absent, except during the larval stage, and the ctenidium is replaced by false gills; abundantly distributed in all seas at present, but owing to their perishable nature are unknown as fossils; and (2) *Tectibranchiata*, in which a mantle, shell, and ctenidium or true gill is developed. To these it will be convenient to add a third group, *Pteropoda*, which is here given nominal rank as a sub-order; as well as a fourth, *Conularida*, to contain Palaeozoic forms of doubtful affinities.

Sub-Order A. TECTIBRANCHIATA.[1]

This group, briefly defined above, has fossil representatives as early as the Palaeozoic. During the Mesozoic, a few genera now extinct were very profuse. Most of the Tertiary species belong to existing genera.

Family 1. Actaeonidae. d'Orbigny.

Shell ovate, with exposed spire, the surface usually grooved and punctured, sometimes smooth. Aperture long, rounded below; columella generally twisted, or with folds. Operculum paucispiral. Carboniferous to Recent.

Solidula, F. de Waldheim (*Buccinulus*, Adams; *Daetylus*, Schum.). Ovate or oblong, compact, solid, with a short conic spire. Columella bearing two plications, the anterior prominent and bifid, the posterior comparatively inconspicuous when the shell is entire; between them the columella is spirally excavated. A few ill-defined species from the French Eocene and Miocene, one from the Australian Pliocene, and numerous recent, tropical species are known.

Fig. 1005.

Tornatellaea simulata, Sowb. Oligocene; Lattdorf, near Bernburg.

Tornatellaea, Conrad (Fig. 1005). Differs from *Solidula* and *Actaeon* in the more anterior disposition of the two columellar plications, in the marked depression on the anterior portion of the aperture, and in the greater thickness of the shell near the outer border of the aperture, which is frequently crenulated. Base of Jura to Miocene; widely distributed. Type—*T. bella*, Conrad. Subgenus—*Triploca*, Tate. Eocene; Australia.

Actaeon, Montf. (*Tornatella*, Lam.; *Speo*, Risso; *Kanilla*, Silvert.). Oval, spirally punctate-striate, with conic spire. Protoconch not very prominent; nucleus sinistral. Columella thick, with one strong, spiral, slightly oblique plication. Upper Cretaceous to Recent.

[1] Literature (see also preceding bibliographies):

Cossmann, M., Essais de Paléoconchologie comparée, I., 1895.

Pilsbry, H. A., Monograph of Recent Tectibranchiata, in Manual of Conchology, vols. XV., XVI. 1894-95.

Adelactaeon, Cossm. (*Myonia*, Adams). Protoconch with sinistral nucleus; not very large. Whorls decussated by fine striae, growth-lines inconspicuous. Columella slightly excavated, and carrying a small but well-marked plication. Miocene of France and Germany, and Recent.

Actaeonina, d'Orb. (*Orthostoma*, Desh.), (Figs. 1006, 1007). Shell ovoid to fusiform, usually smooth, rarely spirally striated.

Fig. 1006.

Actaeonina Dormoisiana, d'Orb. Coral-Rag; Valfin, Ain.

Fig. 1007.

Actaeonina myosotis, Buv. Coral-Rag; St. Mihiel, Meuse. 2/1 (after Buvignier).

Fig. 1008.

Cylindrites acutus, Sowb. sp. Great Oolite; Minchinhampton, England.

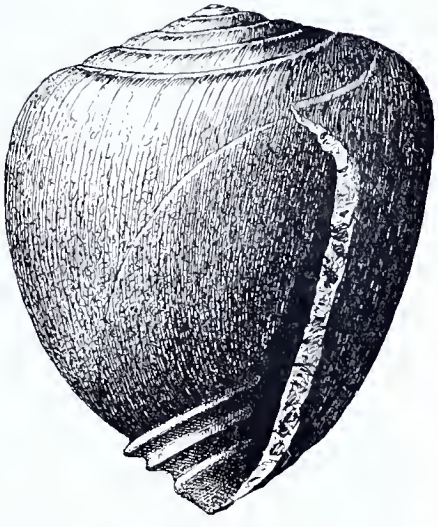


Fig. 1009.

Actaeonella gigantea, Sowb. Turonian; Grünbach, Lower Austria.

Spire conical, body whorl very large, narrowing toward the base. Columella straight, without folds. Outer lip sharp. Carboniferous to Recent.

Sub-genera: *Euconactaeon*, *Conactaeon*, Meek. Lias. *Douvilleia*, Bayle. Tertiary.

Cylindrites, Fer. (Fig. 1008). Cylindrical-ovoid with short spire. Columella with an anterior fold. Trias to Cretaceous.

Bullina, Fer. Jura to Recent. *Cylindrobullina*, v. Ammon. Trias, Lias. *Etallonia*, Desh. Jura and Tertiary. *Bullinula*, Beck. Jura to Recent.

Actaeonella, d'Orb. (Figs. 1009 - 1011). Thick-shelled, inflated, smooth. Spire short; columella thickened anteriorly, with three sharp folds. Very profuse in the Middle and Upper Cretaceous; maximum distribution in the Hippurite Limestone of the Alps.

Sub-genus: *Volvulina*, Stol. (Fig. 1011). Like the preceding, but with insunken spire. Cretaceous.

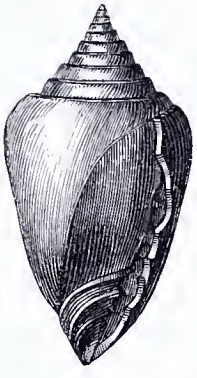


Fig. 1010.

Actaeonella voluta, Goldf. Turonian; Gams, Styria.

Fig. 1011.

Actaeonella (*Volvulina*) *laevis*, Sowb. Turonian; Gosau.

Volvaria, Lam. Cylindrical, with involute, concealed spire. Surface usually spirally striated; aperture narrow; columella with four anterior plications. Eocene.

Family 2. **Ringiculidae.**

Inoperculate forms resembling Actaeonidae in having columellar folds. Cretaceous to Recent.

Cinulia, Gray (Fig. 1012). Globose, inflated, spirally grooved or punctate. Spire short; aperture crescentic; outer lip reflected and thickened. Columella and inner lip with numerous transverse folds. Cretaceous.

Sub-genera: *Avellana*, *Ringinella*, d'Orb.; *Eriptycha*, Meek; *Fortisia*, Bayan. Eocene.

Ringicula, Desh. (Fig. 1013). Small, ovoid to globose, thick-shelled, with mamillated protoconch. Spire short; body whorl large, usually smooth. Aperture canaliculate posteriorly, excavated anteriorly. Columellar border thick and callous; the columella arched, and furnished with from two to four plications. Outer margin usually very thick, reflected, and occasionally denticulated within. Cretaceous to Recent.

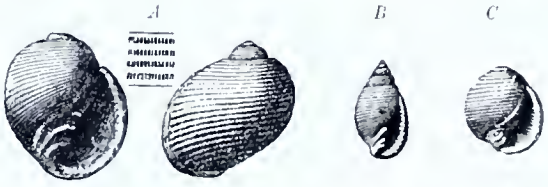


Fig. 1012.

A, *Cinulia* (*Avellana*) *incrassata*, Mant. sp. Gault; Perte du Rhône. *B*, *C*. (*Ringinella*) *lachryma*, Mich. Gault; Folkestone, England. *C*, *C*. (*Eriptycha*) *decurtata*, Zekeli. Turonian. Gosau, Austria.

Fig. 1013.

Ringicula Hoernesi, Seguenza. Miocene; Steinabrunn, near Vienna.

Pugnus, Hedley. Cylindrical, with sunken spire. Recent.

Family 3. **Akeratidae.** Pilsbry.

Shell oval or cylindrical, thin and fragile, the spire low or concealed. Tertiary and Recent.

Akera, Müller (Fig. 1014). Thin-shelled, flexible, with exposed, truncated spire. Whorls separated from one another by deep sutures. Sutures deep and prominent; outer lip separated from the spire. Eocene to Recent.

Haminea, Leach. Oval, thin-shelled, brittle; the spire concealed. Tertiary and Recent.

Fig. 1014.

Akera striatella, Lam. Oligocene; Castel Gomberto, near Vicenza.

Family 4. **Hydatinidae.** Pilsbry.

Globose or oval, with exposed, nearly level spire and tilted nucleus. Jura to Recent.

Hydatina, Leach, Schum. Jura to Recent. *Aplustrum*, Schum.; *Micromelo*, Pilsbry. Recent.

Family 5. **Bullidae.** Pilsbry (emend.).

Shell oval or sub-globose, involute, smooth. Spire sunken and concealed. Aperture long, rounded anteriorly; outer lip sharp. Marine. Jura to Recent.

Bulla, Klein (Fig. 1015). Oval, inflated, with sunken spire and perforate apex. Aperture rounded posteriorly and anteriorly. Jura (?) to Recent.

Fig. 1015.

Bulla ampulla, Linn. Pliocene; Asti, Italy.

Family 6. **Tornatinidae.** Fischer.

Radula unarmed. Tertiary and Recent.

Tornatina, Adams (Fig. 1016). Cylindrical, with projecting spire, and sinistral, tilted nucleus. Columella bearing a single fold. Tertiary and Recent.

Retusa, Brown. Shell resembling *Cylichna*. Tertiary and Recent.

Volvula, Adams (*Volvulella*, Newton). Fusiform, the body whorl forming a point above the spire. Eocene to Recent.

Fig. 1016.

Tornatina exerta, Desh. Oligocene; Jeurres, near Étampes (after Deshayes).

Family 7. **Scaphandridae.**

Spire concealed; radula with few teeth in a row. Trias to Recent.

Scaphander, Montf. (Fig. 1017). Shell sub-cylindrical, with epidermis, usually spirally striated. Body whorl of enormous capacity, much dilated anteriorly. Columella spiral, leaving a false umbilicus. Cretaceous to Recent.

Atys, Montf. Cretaceous to Recent. *Diaphana*, Brown. Tertiary and Recent. *Smaragdinella*, Adams. Recent.

Cylichna, Lovén (*Bullinella*, Newton), (Fig. 1018). Small, cylindrical, solid; spire deeply perforated at the summit; body whorl covering all the others. Aperture very narrow, outer margin longer than the axis of the shell. Columella thickened anteriorly and bearing a small plication; often umbilicated. Trias to Recent.

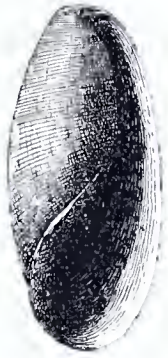


Fig. 1017.

Scaphander conicus, Desh. Eocene; Bracklesham, England.

Fig. 1018.

Cylichna conoidea, Desh. Oligocene; Weinheim, near Alzey.

Family 8. **Philinidae.**

Similar to Scaphandridae, but shell internal, loosely coiled, punctate. Cretaceous to Recent.

Philine, Ascan. (*Bullaea*, Lam.), (Fig. 1019). Cretaceous to Recent.

Fig. 1019.

Philine excavata, Desh. Eocene. Calcaire Grossier; Grignon, near Paris.

Family 9. **Umbraculidae.**

Shell limpet-shaped, with low sub-central apex, and sharp, thin edges. Tertiary and Recent.

Umbraculum, Schum. (*Umbrella*, Lam.). Shell orbicular, broad, patelliform; ornamented exteriorly with concentric lines of growth; internal surface with concentrically undulating striae. Eocene to Recent.

Other families of *Tectibranchiata*, such as *Aplysiidae*, *Pleurobranchidae*, etc., are represented in the recent fauna, but their thin, often membranous shells have not been found fossil. The supposed *Aplysias* reported from the Pliocene by Philippi are flakes from the interior of Pelecypod valves.

Sub-Order B. PTEROPODA. Cuvier.[1]

Naked or shell-covered, hermaphrodite, pelagic Mollusca, without distinct head. Eyes rudimentary, and foot replaced by two lateral, wing-like fins, situated on the anterior end of the body. The gills are placed behind the heart.

The body of these free-swimming Mollusca is sometimes elongated, sometimes coiled posteriorly in a spiral. In some instances it is covered by a thin transparent shell (*Thecosomata*), but oftener it is naked (*Gymnosomata*). The creatures associate in vast swarms in the open sea, and rise to the surface toward nightfall. Their shells often accumulate in prodigious quantities on the sea-bottom, forming calcareous deposits of considerable magnitude.

Cuvier recognised the Pteropods as an independent class of Mollusca, having equal rank with the Gastropods. The researches of Pelseneer, however, have shown that they stand in about the same relationship to the Opisthobranchs as Heteropods do to the Prosobranchs. They are, in fact, Opisthobranchs which have become pelagic, having the foot transformed into a bilobed swimming organ, and with a rudimentary head. The structure of the head is very variable. The heart has only one auricle. Many shell-covered forms (*Limacinidae*) develop a horny operculum, but others are without it.

Fossil Pteropods similar to those now living occur somewhat sparingly in the Upper Cretaceous and Tertiary. Argillaceous strata of Pliocene and Oligocene age are occasionally highly charged with the remains of *Cleodora;* these occur for the most part, however, in a compressed and poorly preserved condition.

Pteropod-like shells are present in the Palaeozoic, appearing as early as the Lower Cambrian (*Conularia*, *Tentaculites*, *Hyolites*), where they constitute an important part of the fauna. These remains were assigned unhesitatingly to the Pteropods by d'Archiac and de Verneuil, Sandberger, Barrande, and numerous other authors. Neumayr, however, and more recently Pelseneer, have urged strong objections against their union with this group, although they have failed to suggest a more satisfactory position for them in the zoological system. Neumayr's proposal to associate the Palaeozoic Tentaculites and Styliolas with Tubicolous Worms was rejected by Nicholson after a microscopic investigation of their shell-structure. The hypothesis advocated by Miller, Fleming, Hall, and more recently by Ihering, according to which Conularias are Cephalopods akin to Orthoceratites, is utterly without any credible foundation.

[1] Literature (see also preceding bibliographies):

Sandberger, G., Die Flossenfüsser oder Pteropoda (Neues Jahrb. für Mineral., pp. 8-25), 1847.

Barrande, J., Pugiunculus, ein fossiles Pteropoden-Geschlecht (Neues Jahrb. für Mineral., pp. 554-558), 1847; Système Silurien du centre de la Bohême, vol. III., Ptéropodes, 1867.

Salter, J. W., Memoirs of the Geological Survey of Great Britain, vols. II., III., 1848, 1866.

Seguenza, G., Paleontologia malacologica dei terreni terziarii del distretto di Messina. Pteropodi ed Eteropodi (Mem. Soc. Ital. Sci. Nat. Milano, vol. II.), 1867.

Karpinsky, A., Die fossilen Pteropoden am Ost-Abhang des Ural. (Mem. Acad. St. Petersburg, ser. 7, vol. XXXII., pp. 1-20), 1884.

Dollfus, G., and *Ramond, G.*, Liste des Ptéropodes du terrain tertiare parisien (Mem. Soc. Malacol. de Belgique, vol. XX.), 1885.

Walcott, C. D., Contribution to Studies on the Cambrian Faunas of North America (Bull. U.S. Geol. Survey, vol. IV., No. 30, pp. 125-146), 1886; The Fauna of the Lower Cambrian or Olenellus Zone (Tenth Ann. Rept. U.S. Geol. Survey), 1890.

Pelseneer, P., Report on the Pteropoda (Report Challenger Expedition, Zoology, vol. XXIII.), 1888; Bull. Soc. Belge de Geol. Palaeont. et Hydrol., vol. III. p. 124), 1889.

Blanckenhorn, M., Pteropodenreste aus der oberen Kreide Nord-Syriens und aus dem hesseschen Oligocän (Zeitschr. deutsch. geol. Gesellsch., vol. XLI. pp. 593-602), 1889.

Novák, O., Revision der palaeozoischen Hyolithiden Böhmens (Abhandl. böhm. Gesellsch. Wissensch. [7] Bd. IV.), 1891.

Holm, G., Sveriges Kambrisk-Siluriska Hyolithidae och Conulariidae (Afhandl. Sver. geol. Undersökning, Ser. C, No. 112), 1893.

It manifestly cannot be denied that Conularias and Hyolithes in particular, as regards size, shell structure, and probably also conditions of existence, differed considerably from recent Pteropods. But in spite of the differences so strongly emphasised by Pelseneer, the fact remains that of all shell-covered organisms, they approach the Pteropods most nearly, and cannot with propriety be referred to any other group of the Mollusca.

Family 1. **Limacinidae.** Gray.

Shell thin, spiral, sinistral, with vitreous, paucispiral operculum. Tertiary and Recent.

The genus *Limacina*, Lam. (*Spirialis*, Eyd. and Soul.; *Embolus*, Jeffreys), is of sporadic occurrence in the Tertiary (Eocene and Pliocene). *Valvatina*, Watelet, includes flat sinistral shells from the Calcaire Grossier of Paris, and *Planorbella*, Gabb, contains similar forms from the Oligocene of San Domingo.

Family 2. **Cavoliniidae.** Fischer.

Shell symmetrical, thin, vitreous, ventricose, pyramidal, or conically tubiform, but not spiral. Cretaceous to Recent.

Cavolinia, Gioeni (*Hyalaea*, Lam.; *Gamopleura*, Bellardi), (Fig. 1020). Shell globose, laterally keeled and slit, acuminate posteriorly; composed of two unequally arched pieces, one of which projects helmet-like above the other. Recent, and fossil in the Italian Miocene and Pliocene.

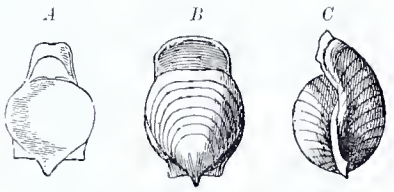


Fig. 1020.

A, *Cavolinia* (*Hyalaea*) *tridentata*, Forsk. Recent. *B*, *C*, *C.* (*Gamopleura*) *taurinensis*, Sism. Miocene; Turin, Italy.

Clio, Linn. (*Cleodora*, Péron and Lesueur; *Balantium*, Benson; *Flabellum*, *Poculina*, Bellardi), (Fig. 1021). Shell somewhat angular, compressed dorso-ventrally, with lateral keels. A crest or rib generally extends longitudinally along the back, and usually projects. Upper Cretaceous to Recent. A common fossil in the Pliocene of Monte Mario, near Rome, and the vicinity of Messina and Turin; also in the Oligocene of the Mayence Basin, and in the English Crag.

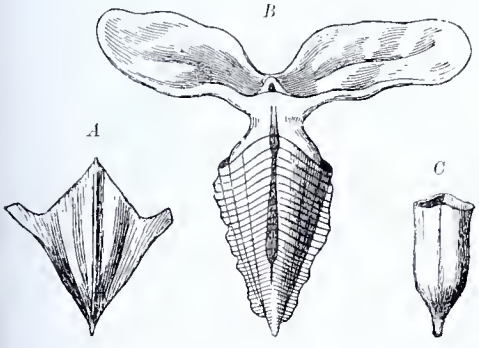


Fig. 1021.

A, *Cleodora pyramidata*, Linn. Pliocene; Monte Mario, near Rome. *B*, *Balantium recurvum*, A. Adams. Recent. Animal with shell (after Adams). *C*, *Vaginella depressa*, Daudin (*Cleodora strangulata*, Desh.). Miocene; Dax, near Bordeaux.

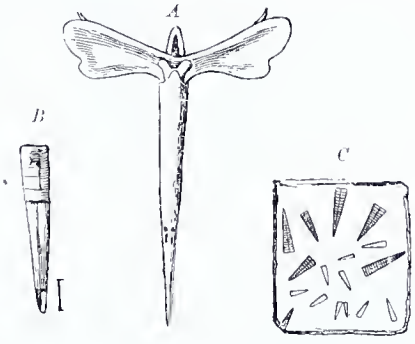


Fig. 1022.

A, *Styliola recta*, Lesueur. Recent (after Adams). *B*, *Styliola striatula*, Novák. Devonian (Étage H); Hlubocep, Bohemia. $^3/_1$. *C*, *Styliola clavulus*, Barr. Devonian (Étage H); Hostin, near Prague, Bohemia. Several individuals on slate-fragment. $^1/_1$.

Sub-genus: *Styliola*, Lesueur (*Creseis*, Rang; *Crisia*, Menke), (Fig. 1022). Shell conical,

straight, elongated ; surface smooth or faintly striated ; dorsal groove not parallel to axis of the shell, but slightly oblique, with only the anterior extremity (which ends in a rostrum) in the median line ; embryonic portion ends in a pointed apex. Tertiary and Recent.

In the Devonian of Bohemia, Nassau, Ural, and North America, great numbers of smooth, circular, longitudinally striated tubes are occasionally met with, the posterior end of which is inflated into a small bulb. Similar tubes have also been described by Blankenhorn from the Cretaceous of Syria. None of these differ externally to any great extent from *Clio* or *Styliola*.

Vaginella, Daudin (Fig. 1021, *C*). Shell long, ventricose, depressed ; apex sharp-pointed, constricted in front ; aperture slightly canaliculated and compressed laterally. Cross-section elliptical. Upper Cretaceous to Recent.

Curicria, Rang ; *Triptera*, Quoy (*Fibiella*, O. Meyer). Tertiary and Recent. *Euchilotheca*, Fischer. Eocene.

Sub-Order C. CONULARIDA. Miller and Gurley.

Palæozoic forms of doubtful systematic position, resembling some recent Pteropoda, but probably to be regarded as a parallel rather than as an identical group.

Family 1. Tentaculitidae. Walcott.

Thick-walled, tapering, elongate, conical tubes, having a circular cross-section, and terminating posteriorly either acutely or in an embryonal bulb. Surface ornamented with parallel raised transverse rings. The apical portion of the shell often filled with calcareous matter, or divided off by transverse septa. Ordovician to Devonian.

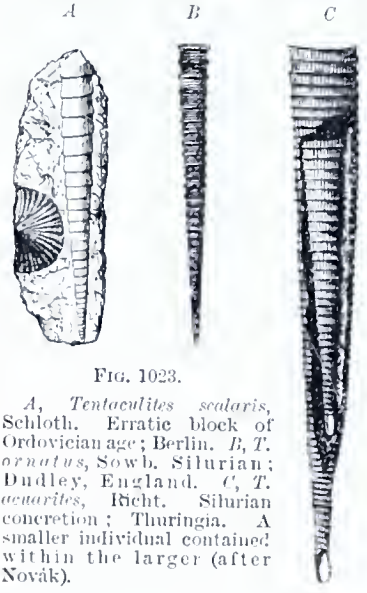


Fig. 1023.

A, *Tentaculites scalaris*, Schloth. Erratic block of Ordovician age ; Berlin. *B*, *T. ornatus*, Sowb. Silurian ; Dudley, England. *C*, *T. acuarites*, Richt. Silurian concretion ; Thuringia. A smaller individual contained within the larger (after Novák).

Tentaculites, Schloth. (Fig. 1023). This, the solitary genus, is prodigiously abundant in the Silurian and Devonian, the strata being sometimes fairly charged with their remains. The shell is composed of a compact outer layer, and an inner layer made up of thin lamellæ running parallel with the external surface. The supposed Tentaculites described from the Oligocene by Ludwig and Blankenhorn are thin-shelled, transversely ribbed, conical tubes, which probably belong in the neighbourhood of *Styliola* or *Euchilotheca*.

Family 2. Torellellidae. Holm.

Thick-walled, smooth, transversely or longitudinally striated, straight or bent tubes, acutely terminated posteriorly, and without opercula. Cambrian to Silurian.

Torellella, Holm. Tubes strongly compressed, flattened at both ends, elliptical in cross-section, and with fine transverse striæ ; composed of brownish-coloured calcium phosphate. Cambrian to Silurian ; Sweden.

Hyolithellus, *Salterella*, Billings, *Coleolus*, Hall, and *Coleoloides*, Walcott, from the Lower Cambrian of North America, probably also belong here.

Family 3. Hyolithidae. Nicholson.

Shell symmetrical, conical, or pyramidal, straight or sharply bent ; cross-section triangular, elliptical, or lenticular ; one side often flattened, and the other arched or with

a blunt median keel. Surface smooth or with fine transverse striae, rarely longitudinally striated or ribbed. Aperture completely closed by an operculum, the latter being semicircular, triangular, or lentiform, with lateral nucleus, and concentrically striated. Cambrian to Permian.

The shells belonging here are of large size, and composed of calcium carbonate. The posterior portion is often divided off by transverse septa.

According to Holm, the typical genus *Hyolithes*, Eichwald (*Theca*, Sowb.; *Pugiunculus*, Barr), (Fig. 1024), is divisible into two sub-genera. One of these, *Orthotheca*, Novák, contains forms with an abruptly truncated anterior end; and in the other, *Hyolithes*, s. str., the margin of the flattened side projects somewhat above the opposite wall. The forms known as *Cleidotheca*, *Centrotheca*, Salter; *Camerotheca*, *Diplotheca*, Matthew; *Pharetrella*, Hall; *Ceratotheca* and *Bactrotheca*, Novák, fall within the synonomy of *Hyolithes*. This genus is abundantly distributed in the Cambrian, Ordovician, and Silurian of North America, Great Britain, Sweden, Russia, and Bohemia; it occurs sparingly also in the Devonian, Carboniferous, and Permian.

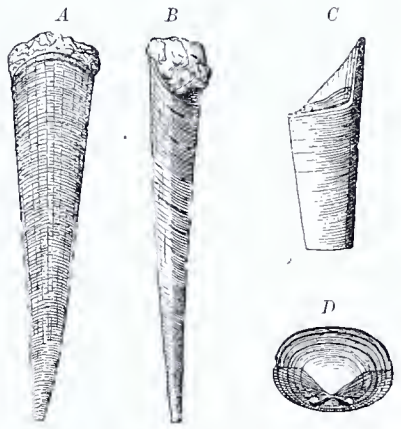


Fig. 1024.

A, B, Hyolithes elegans, Barr. Ordovician; (Étage D); Lodenice, Bohemia. Slightly reduced. *C, H. maximus*, Barr. Cambrian (Étage C); Mleschitz, Bohemia. Anterior portion restored, with operculum; viewed from the side, 1/2. *D*, Operculum (after Barrande).

Pterotheca, Salter; Silurian. *Matthewia*, Walcott. *Phragmotheca*, Barrande. Cambrian.

Fig. 1025.

Conularia anomala, Barr. Ordovician (Étage D); Drabov, Bohemia.

Fig. 1026.

Conularia quadrisulcata, Sowb. Upper Carboniferous Limestone; Glasgow, Scotland. Showing well-preserved apertural margins (after Etheridge).

Family 4. **Conulariidae.** Walcott.

Shell rectilinear, inversely conical, rectangular to rhombic in cross-section, with usually sharp edges, acute or truncated posteriorly. Each of the transversely striated or ribbed lateral faces divided into longitudinal halves by a superficial groove, corresponding internally to a median ridge. Posterior portion of the shell divided off by septa. Aperture constricted by four triangular or linguiform incurved lobes of the anterior margin. Ordovician to Jura.

Conularia, Mill. (Figs. 1025, 1026). This, the solitary genus, sometimes attains a length of 20 cm., and is represented by about 100 species. Its maximum distribution occurs in the Ordovician and Silurian of Bohemia, Normandy, England, Sweden, and North America, and in the Devonian of North America and Bolivia. It is rare in the Carboniferous and Permian, and the last surviving species occurs in the Trias and Lias.

Order 2. PULMONATA. Cuvier. Air-breathing Snails.[1]

Euthyneura in which the gill cavity is transformed into a lung for breathing free air. Mainly terrestrial or fresh-water forms.

A few Pulmonates have reverted to exclusively aquatic habits, and have the lung filled with water; and in a few, secondary gills are developed in the cavity. These, however, are rare exceptions. The great majority of forms breathe air by means of a network of blood-vessels spread upon the inner surface of the lung. The ordinary aquatic forms come to the surface of the water at intervals to renew their supply of air. They have, with few exceptions, no operculum, and the shell is often vestigeal or absent.

Next to the Prosobranchs the Pulmonates are the largest group of Gastropods, there being upwards of 6000 living and 700 fossil species known. The most important and highly diversified genera (*Helix*, *Bulimus*, *Clausilia*) are terrestrial in habit; certain others (*Planorbis*, *Limnaea*, *Physa*) are confined to fresh water. The oldest Pulmonates are of rare occurrence in the Devonian and Carboniferous; they are found sparingly in the Jura and Cretaceous, are of greater abundance in the Tertiary, but do not attain their maximum distribution until the present geological period.

The *Thalassophila* and *Auriculidae* are restricted to marine deposits; remaining Pulmonates are rarely found outside of fresh-water strata, and are commonly associated with other fresh-water organisms that have been swept by rainfall or running water into swamps or estuaries.

Sub-Order A. THALASSOPHILA. Gray.

Shell either spiral and operculate, or bowl-shaped to depressed conical, without spire, and somewhat unsymmetrical. Animal usually provided with a single gill in addition to the lung cavity. Tentacles fused with the discoidal head. Eyes sessile.

The *Thalassophila* inhabit the littoral zone of the ocean and brackish estuaries. Fossil remains occur from the Devonian onward. Three families are recognised—*Siphonariidae*, *Gadiniidae*, and *Amphibolidae*; but these are not readily distinguishable by shell characters alone.

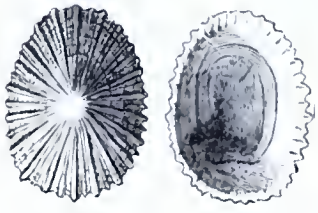


Fig. 1027.

Siphonaria crassicostata, Desh. Eocene; Anvers, near Paris.

Fig. 1028.

Hercynella bohemica, Barr. Devonian (Étage F); Lochkow, Bohemia.

Siphonaria, Blainville (Fig. 1027). Shell usually radially ribbed. Apex directed backwards or toward the left side; internally with two unequal muscular impressions, which are interrupted on the right side in front by a broad groove. Tertiary and Recent.

Hercynella, Kayser (Fig. 1028). Devonian. *Anisomyon*, Meek and Hayden. Jura and Cretaceous.

Valenciennesia, Rousseau. Shell very thin, broadly bowl-shaped, concentrically ribbed. Apex situated near the posterior margin. Right side bearing a broad

[1] *Sandberger*, *F.*, Land- und Süsswasser-Conchylien der Vorwelt. 1870-75.
White, *C. A.*, Review of American non-marine Mollusca.
Tryon, *G. W.* and *Pilsbry*, *H. A.*, Manual of Conchology, *Pulmonata*.

plication for the respiratory tube. Found in brackish water, Congerian Stage (Pliocene), of Hungary, Roumania, and South Russia.

Williamia, Monts.; *Gadinia*, Gray. Recent and Pliocene.

Amphibola, Schum. Shell spirally globose, thick, rugose, and operculate. Recent. This is placed in a separate family, *Amphibolidae*.

Sub-Order B. BASOMMATOPHORA. A. Schmidt.

Shell invariably present. Eyes situated at the base of a pair of tentacles. Aquatic, or living in the vicinity of water.

Family 1. **Auriculidae.** Blainville.

Shell thick, ovate. Spire short, body whorl very large. Inner lip or columella bearing plications. Shore forms or inhabitants of salt marshes. Jura to Recent.

Auricula, Lam. (Fig. 1029). Elongate-oval, with epidermis. Aperture narrow, rounded anteriorly. Inner lip bearing two or three folds; outer lip thickened, sometimes denticulated. Jura to Recent.

Fig. 1029. *Auricula Dutemplei*, Desh. Lower Eocene; Sainceux (after Deshayes).

Fig. 1030. *Alexia pisolina*, Desh. Miocene; Pontlevoy, Touraine. 2/1.

Fig. 1031. *Pythiopsis Lamarcki*, Desh. sp. Eocene; Houdan (after Deshayes).

Fig. 1032. *Carychium antiquum*, A. Braun. Miocene; Hochheim, near Mayence. Enlarged.

Cassidula, Fer.; *Plecotrema*, Adams; *Alexia*, Leach (Fig. 1030); *Pythiopsis*, Sandb. (Fig. 1031); *Melampus*, Montf.

Carychium, Müll. (Fig. 1032). Shell small, smooth, and glossy. Inner lip bearing one or two folds; outer margin thickened, sometimes with a tooth. Jura to Recent.

Scarabus, Montf. (*Polyodonta*, Fischer and Waldh.); *Leuconia*, Gray; *Blauneria*, Shuttleworth, etc. Tertiary and Recent.

Fig. 1033. *Physa gigantea*, Michaud. Lower Eocene; Rilly, near Rheims.

Family 2. **Chilinidae.** Dall.

Shell oval, auriculate, with large aperture, the columellar margin provided with spiral folds; surface coloured in various patterns. Tertiary and Recent.

Chilina, Gray. This is said to be Streptoneurous. The dentition resembles that of *Physa*. Miocene and Recent; South America.

Family 3. **Physidae.** Dall.

Shell sinistral, oval, glossy, unicoloured. Aperture large; columella twisted or simple. Jura to Recent.

Physa, Drap. (Fig. 1033). Shell resembling *Limnaea*, but sinistral. Upper Jura to Recent.

Family 4. **Limnaeidae.** Keferstein.

Shell thin, turreted, or discoidal. Fresh-water inhabitants. Lias to Recent; especially abundant in the Tertiary.

Limnaea, Lam. (*Limnaeus*, auct.), (Fig. 1034). Shell so thin as to be translucent. Body whorl very large; spire acute, and moderately high. Aperture wide, oval; outer margin sharp. Upper Jura (Purbeck) to Recent; maximum in Tertiary.

Fig. 1034.

Limnaeus pachygaster, Thom. Fresh-water Miocene; Mörsingen, near Ulm.

Fig. 1035.

Planorbis cornu, Brongt. var. *Mantelli*, Dunker. Upper Miocene; Mmmdingen, Würtemberg.

Planorbis, Guettard (Figs. 1035, 1036). Discoidal (exceptionally turreted), with many whorls. Aperture oval to crescent-shaped; outer margin sharp. Lias to Recent; very profuse in the Tertiary. *P. multiformis*, Bronn sp., from the Middle Miocene of Steinheim in Würtemberg, is particularly interesting on account of its extraordinary variability. The different mutations of the species are usually found at different horizons of the fresh-water limestone occurring

Fig. 1036.

Planorbis multiformis, Bronn sp. Upper Miocene fresh-water limestone; Steinheim, near Heidenheim, Würtemberg. *A*, var. *suprema*. *B*, var. *trochiformis*. *C*, var. *elegans*. *D*, var. *steinheimensis*.

there, and constitute, according to Hilgendorf and Hyatt, a remarkable genealogical sequence.

Isidora, Ehr. Shell similar to that of *Physa*. Recent; tropical countries.

Family 5. **Ancylidae.**

Shell limpet-shaped, conical, not spiral, or with the apex recurved. Tertiary and Recent.

Ancylus, Geoffrey (Fig. 1037). Shell simply conic or with the apex slightly incurved. Tertiary and Recent.

Gundlachia, Pfeiff. An accessory shell at the apex of the principal one. Tertiary of Mayence Basin and Recent.

Fig. 1037.

Ancylus Dutemplei, Desh. Calcaire Grossier; Boursault.

Sub-Order C. TELETREMATA. Pilsbry.

Shell absent; mantle covering the whole upper surface of the body. Male and female orifices widely separated; lung orifice and anus central and near the tail.

Several families of this sub-order are recognised (*Vaginulidae*, *Rathouisiidae*, *Onchidiidae*), but owing to the absence of a shell, their remains are not preservable in the fossil state.

Sub-Order D. STYLOMMATOPHORA. A. Schmidt. Land Snails.

Eyes borne on the extremities of two peduncles, which are capable of invagination; a pair of short tentacles, rarely obsolete, are placed in front of them. Male and female genital orifices contiguous, or uniting in a common vestibule, situated at the right or

left side of the head. Buccal retractors present; lung foramen and anus anterior to end of foot, not ventral.

This sub-order comprises most recent and all fossil land snails, and is divisible into series or superfamily groups. The families proper are based almost wholly upon characters of the soft anatomy, which are herein largely omitted or abridged.

Superfamily 1. HOLOPODA. Pilsbry.

No longitudinal grooves above the margins of the foot; jaw present, teeth quadrate.

Family 1. Helicidae. Keferstein. Helices.

Shell depressed, globose, or oval and elevated. Tertiary and Recent.

This comprises an enormous assemblage in the recent fauna, but most of the genera have not as yet been found fossil. All the typical forms will probably in time be traced back to the Eocene. Sub-family and generic characters are based largely upon the genital system, and hence are of little practical importance to the palaeontologist.

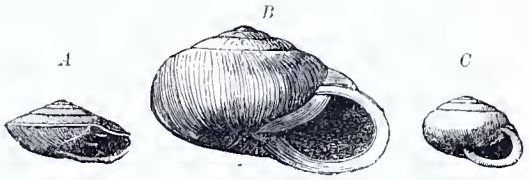


FIG. 1038.

A, Dimorphoptychia Arnouldi, Michaud. Lower Eocene; Rilly, near Rheims. *B, Helix* (*Campylaea*) *inflexa*, Klein. Upper Miocene; Mörsingen. *C, Helicodonta osculum*, Thom. Lower Miocene; Hochheim, near Wiesbaden.

Polygyra, Say. Globose or depressed, with the lip reflected, often toothed. Miocene to Recent; North America.

Sagda, Beck. Glossy, with many close whorls, the last usually with internal laminae and a sharp lip. Oligocene to Recent; Antilles.

Plcurodonte, Fisch. de Wald. Solid, large, depressed, and generally keeled; aperture often toothed. Oligocene to Recent; Antilles, Florida.

Helix, Linn. (Fig. 1038, *A*, *B*). Shell semi-globose, conical to discoidal, manifesting great variability of form. Aperture oblique, crescentic or rounded, with disconnected margins. Very profuse in the Tertiary and Recent of Europe and adjacent regions of Asia and Africa.

Helicodonta, Fer. (Fig. 1038, *C*). Similar to *Helix*, but with thickened or denticulated lip. Oligocene to Recent; Europe.

Other allied genera occur in European Tertiary deposits. Recent *Helicidae* reproducing by extraordinarily large eggs are the following:—*Helicophanta* of Madagascar; *Acavus*, Ceylon; *Panda*, Australia; *Strophocheilus*, South America.

FIG. 1039.

A, Clausilia bulimoides, A. Braun. Lower Miocene; Eckingen, near Ulm. *B, C. antiqua*, Schübler. Same locality.

Family 2. Bulimulidae. Fischer.

Shell elongated, ovate, with narrow umbilicus or none. Tertiary and Recent.

Bulimulus, Leach. Miocene to Recent; America. *Amphidromus*, Alb. Tertiary; Europe and Asia.

Family 3. Pupidae.

Shell small, cylindrical or oval, with narrow whorls. Tertiary and Recent.

Clausilia, Drap. (Fig. 1039). Shell turreted to fusiform, slender, sinistral. Aperture pyriform, with usually continuous peristome. Inner lip

bearing two folds; outer margin somewhat reflected; the aperture usually closed by a movable calcareous plate. Occurs sparingly fossil from the Eocene onward, and represented by about 400 recent species.

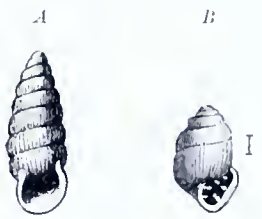


Fig. 1040.

A, *Dendropupa vetusta*, Dawson. Coal Measures; Nova Scotia (after Dawson). *B*, *Pupa diversidens*, Sandb. Miocene; Sansan, Gers (after Sandberger).

Fig. 1041.

Buliminus (*Petraeus*) *complanatus*, Reuss. Lower Miocene; Thalfingen, near Ulm.

Pupa, Lam. (Fig. 1040, *B*). Shell small, cylindrical-ovate. Aperture semicircular, usually constricted by teeth on the columella and inner and outer lips. The outer margin reflected. Tertiary and Recent.

Dendropupa, Dawson (Fig. 1040, *A*). Like the last, but aperture without teeth. Carboniferous; Nova Scotia.

Vertigo, Müller. Tertiary and Recent.

Buliminus, Ehrb. (Fig. 1041). High conic, solid, turreted. Eocene to Recent.

Family 4. **Achatinidae.**

Ovate or elongate, imperforate shells, with the columella generally truncated at the base. Upper Cretaceous to Recent.

Achatina, Lam. Recent; tropical Africa.

Stenogyra, Shuttlew.; *Rumina*, Risso; *Opeas*, Alb.; *Rhodea*, Adams. These are all small members of the group, mainly Recent.

Megaspira, Lea (Fig. 1042). Turreted, slender, very long; columella with transverse folds. Upper Cretaceous to Recent.

Cionella, Jeffreys; *Azeca*, Leach; *Caecilianella*, Bourg., etc. Tertiary and Recent.

Fig. 1042.

Megaspira exarata, Mich. sp. Lower Eocene; Rilly, near Rheims.

Superfamily 2. AGNATHA. Mörch.

Carnivorous snails, usually with no jaw, thorn-shaped teeth, and without furrows above the foot-edges.

Fig. 1043.

Testacella Zellii, Klein. Miocene; Andelfingen (after Sandberger).

Family 1. **Testacellidae.** Gray.

Shell spiral, of very small size, and situated near the tail of the vermiform animal. Tertiary and Recent.

Testacella, Cuv. (Fig. 1043). Shell auriform, borne on the posterior end of the animal. Tertiary and Recent.

Parmacellina, Sandb. Eocene. *Daudebardia*, Hartm. (*Helicophanta*, Fér. p.p.). Quaternary and Recent.

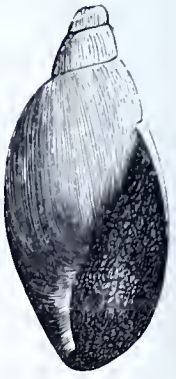


Fig. 1044.

Glandina inflata, Reuss. Miocene; Richelberg, near Ulm.

Family 2. **Glandinidae.**

Shell oval or oblong, capable of containing the entire animal. Cretaceous to Recent.

Glandina, Schum. (Fig. 1044). Shell elongate-oval, with high spire. Aperture notched in front; columella truncated. Upper Cretaceous to Recent. Other recent allied genera inhabit the American tropics.

Superfamily 3. AULACOPODA. Pilsbry.

Foot with longitudinal grooves above and parallel with its lateral margins.

Family 1. Zonitidae.

Aulacopoda with a spiral, conic, or helicoid shell, sometimes partially uncoiled, usually smooth and with simple lip; marginal teeth of the radula thorn-like; foot margin wide; jaw rather smooth. Carboniferous (?) to Recent.

Vitrina, Drap. Shell small, translucent, with short spire, and very large body whorl. Tertiary and Recent.

Archaeozonites, Sandb. (Fig. 1045). Thick-shelled, globose, with rather high spire, deeply umbilicate; outer margin sharp. Oligocene and Miocene. Here also should

Fig. 1045.

Archaeozonites subverticillus, Sandb. Lower Miocene; Eckingen, near Ulm.

Fig. 1046.

Hyalina denudata, Reuss sp. Miocene; Tuchoritz, Bohemia.

Fig. 1047.

Lychnus Matheroni, Requien. Upper Cretaceous (Garumnian); Rognac, Provence.

be placed, perhaps, the archaic *Helix*-shaped snails from the Coal Measures of Nova Scotia.

Zonites, Montf. Like the last, but with thinner shell, granulated above, and smooth below. Tertiary and Recent.

Hyalina, Fér. (Fig. 1046); *Omphalosagda*, Sandb.; *Ariophanta*, Desm.; *Trochomorpha*, Albers. Tertiary and Recent.

Lychnus, Montf. (Fig. 1047). Body whorl large, bent upward at first, and later decurved, so that the margins of the aperture lie in the basal plane. Upper Cretaceous of Provence and Spain.

Family 2. Limacidae. Lamarck.

Naked slugs having a small vestigeal shell, flat and non-spiral, concealed within the mantle, which latter forms a small oval shield on the forepart of the body. Foot margin narrow; dentition and jaw as in the Zonitidae. Tertiary and Recent.

The principal genera are *Limax*, Linn., in which the intestine has four longitudinal folds, and the back is keeled at the tail only; and *Amalia*, Moq.-Tand., with spiral gut and strongly keeled back. Their small scale-like shells have been found in the Tertiary and Pleistocene; present distribution nearly world-wide.

Family 3. Endodontidae. Pilsbry.

Shell spiral and external, varying from cylindric to helicoid and planorboid, usually rib-sculptured and with opaque colouring; lip thin, unexpanded. Jaw of separate or united imbricating plates, or solid and striated; marginal teeth squarish; genitalia without accessory organs. Carboniferous to Recent.

Punctinae. Jaw of numerous separate plates; shell minute. Includes the Holarctic genera *Punctum*, Morse, and *Sphyradium*, Charp., and the New Zealand genus *Laoma*, Gray. Recent.

Endodontinae. Jaw-plates united more or less completely. Genera: *Pyramidula*, Fitz. Discoidal or low conic, with tubular ribbed whorls and open umbilicus. Carboniferous to Recent. This is one of the most ancient land Mollusks known, and is the oldest Helicoid form. *Phasis*, *Amphidoxa*, *Flammulina*, and *Endodonta*, Alb., are similar austral forms, but are only known Recent.

Family 4. Arionidae.

Slugs having the shell reduced to a flat plate or a few granules, nearly or entirely concealed, or absent. Mantle in the form of a shield on anterior part of the body; teeth of the quadrate type. Recent.

This family is probably derived from the *Endodontidae* by degeneration of the shell. *Arion*, Fér., and *Anadenus*, Heyn., are leading genera of Europe and Asia; *Ariolimax*, Mörch., and *Prophysaon*, Bland, those of North America.

Family 5. Philomycidae.

Slugs somewhat similar to Arionidae, but the mantle covers the entire upper surface of the body. A shell is completely absent; hence no fossil forms are known.

Superfamily 4. ELASMOGNATHA. Mörch.

Jaw with a strong squarish process of attachment above.

Fig. 1048.

Succinea peregrina, Sandb. Lower Miocene; Tuchoritz, Bohemia.

Family 1. Succineidae.

Shell thin, ovate, consisting of few whorls.

Succinea, Pfeiffer (Fig. 1048). Shell thin, ovate, amber-coloured, translucent, with short spire, and large body whorl. Outer margin of aperture sharp. Tertiary and Recent; abundant in the Loess.

Range and Distribution of the Gastropoda.

Of all classes of Mollusks, the Gastropods exhibit the most manifold variety. Beginning in the Cambrian, they acquire a very gradual increase and distribution, and are at present enjoying their maximum vigour. There exist probably over 20,000 recent species, about three-fifths of which have gills, the remainder being air-breathers.

At the base of the Cambrian (Olenellus zone) are found such archaic genera as *Scenella*, *Stenotheca*, *Platyceras*, *Rhaphistoma*, *Pleurotomaria*, and a number of doubtful Pteropod-like forms (*Hyolithes*, *Hyolithellus*, *Salterella*, *Torellella*, etc.), which evince the great antiquity of the Aspidobranchs and forms resembling the *Capulidae*. In the later Cambrian the *Rhipidoglossa* (represented by the *Pleurotomariidae*, *Euomphalidae*, and *Bellerophontidae*) predominate; and associated with these are certain Pteropod remains, members of the *Capulidae*, and a few genera probably referable to the *Turbinidae*. A notable genus occurring here is *Subulites*, which bears some resemblance to the *Pyramidellidae*, and exhibits a distinct channelling at the base of the columella.

Unfortunately the poorly preserved remains of Cambrian Gastropods afford

but scanty information regarding the disposition of the soft parts; nevertheless, there are good, although purely theoretical reasons for supposing that the *Rhipidoglossa* and Ctenobranchs were formerly not so widely separated as at present.

During the Ordovician and Silurian, Gastropods increased perceptibly in the number of species, and a few new families were initiated (*Scalariidae*, *Purpurinidae*, *Trochidae*, *Xenophoridae*); but the faunal aspect remained on the whole much the same as in the Cambrian, and no essential changes were introduced during the remainder of the Palaeozoic. Accordingly, the Palaeozoic Gastropod fauna may be said to be characterised by its general simplicity, being made up principally of so-called Pteropods, *Rhipidoglossa*, a few *Docoglossa* and Opisthobranchs, and also a scattering representation of Ctenobranchs (*Capulidae*, *Pyramidellidae*, *Littorinidae*).

During the Jura-Trias, the large, thick-shelled varieties of Pteropod-like Mollusks became extinct. But, on the other hand, various families of the *Rhipidoglossa* reached the acme of their development (*Pleurotomariidae*, *Turbinidae*, *Neritopsidae*, *Neritidae*); and among the Ctenobranchs, the families *Pyramidellidae*, *Nerineidae*, *Purpurinidae*, *Turritellidae*, and *Aporrhaidae* multiplied in a great variety of forms.

The Cretaceous witnessed a decided increase among the siphonostomous Ctenobranchs, and in the Tertiary this branch asserted itself as the dominant type of Gastropods, surpassing all other families in point of numbers, and gradually acquiring the aspect of living genera and species. The *Nerineidae*, *Pyramidellidae*, and *Aporrhaidae*, which played such a prominent rôle along with the *Rhipidoglossa* during the Mesozoic era, became in part extinct in the Tertiary, and the remainder entered upon their decline. The great majority of Eocene and Oligocene genera are still living, but the species have almost without exception become extinct. During the Miocene, a few species made their appearance which are still in existence, and of the Pliocene species, between 80 and 90 per cent are represented in the recent fauna.

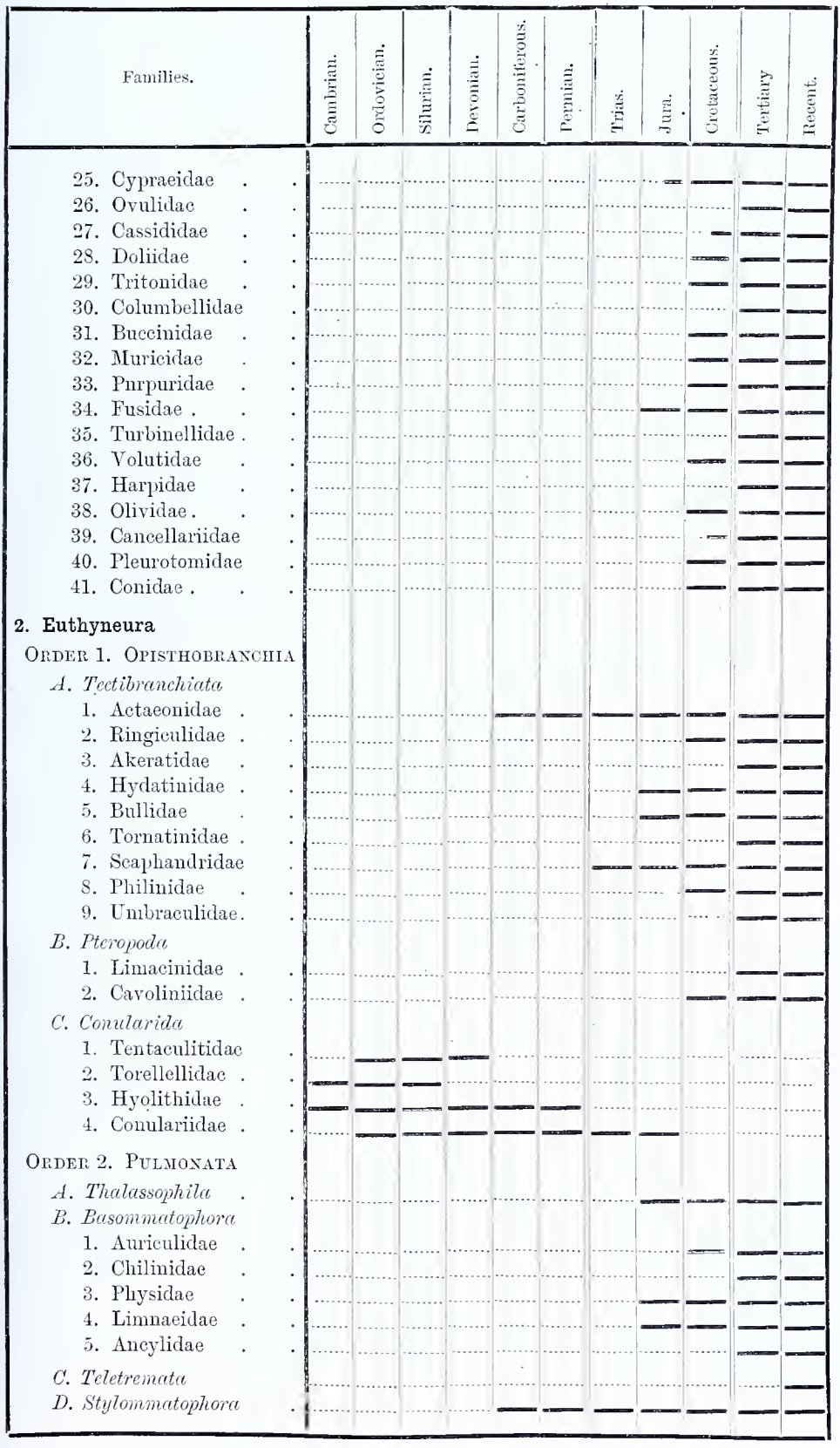
The geological history of the *Pulmonata* is remarkable. Thalassophilous *Siphonariidae* are first met with in the Devonian, where they are very sparse. Land snails (*Archaeozonites*, *Pyramidula*, *Dendropupa*) were initiated in still smaller numbers during the Carboniferous; but not until the boundary between the Jura and Cretaceous is reached do we find any traces of fresh-water snails. We meet them first in the Purbeck. In the Wealden, and Cretaceous generally, both land and fresh-water Gastropods are quite abundant; they became highly developed and widely distributed during the Tertiary, attaining, in fact, a differentiation nearly equal to that exhibited by the corresponding recent forms.

The successive approximations to present conditions among Gastropod faunas have not been confined to the production of forms simulating more and more those now living; they include also the gradual demarcation of existing geographical provinces. Mesozoic Gastropods are too dissimilar in their general characters to admit of a close comparison with modern faunas; but as early as the Eocene resemblances to modern forms are observable, and a certain correspondence is to be noted with Gastropods now inhabiting somewhat warmer zones.

The Eocene faunas of Europe, North America, Asia, and Northern Africa share a great many species in common, and have numerous others which are

TABLE SHOWING THE VERTICAL RANGE OF THE GASTROPODA.

Families.	Cambrian.	Ordovician.	Silurian.	Devonian.	Carboniferous.	Permian.	Trias.	Jura.	Cretaceous.	Tertiary.	Recent.
1. Streptoneura											
ORDER 1. ASPIDOBRANCHIA											
A. Docoglossa											
B. Rhipidoglossa											
1. Haliotidae											
2. Pleurotomariidae											
3. Bellerophontidae											
4. Fissurellidae											
5. Euomphalidae											
6. Stomatiidae								?			
7. Turbinidae											
8. Phasianellidae											
9. Delphinulidae											
10. Trochonematidae											
11. Trochidae											
12. Umboniidae											
13. Neritopsidae											
14. Neritidae											
ORDER 2. CTENOBRANCHIA											
A. Heteropoda											
B. Platypoda											
1. Eulimidae											
2. Pyramidellidae											
3. Scalariidae											
4. Solariidae											
5. Purpurinidae											
6. Littorinidae											
7. Cyclostomidae											
8. Capulidae											
9. Naticidae											
10. Xenophoridae											
11. Ampullariidae											
12. Valvatidae											
13. Viviparidae											
14. Amnicolidae											
15. Rissoidae											
16. Turritellidae											
17. Vermetidae											
18. Caecidae											
19. Melaniidae											
20. Nerineidae											
21. Cerithiidae											
22. Aporrhaidae											
23. Strombidae											
24. Columbellinidae											


Families.
Cambrian.
Ordovician.
Silurian.
Devonian.
Carboniferous.
Permian.
Trias.
Jura.
Cretaceous.
Tertiary
Recent.
25. Cypraeidae
26. Ovulidae
27. Cassididae
28. Doliidae
29. Tritonidae
30. Columbellidae
31. Buccinidae
32. Muricidae
33. Purpuridae
34. Fusidae
35. Turbinellidae
36. Volutidae
37. Harpidae
38. Olividae
39. Cancellariidae
40. Pleurotomidae
41. Conidae
2. Euthyneura
Order 1. Opisthobranchia
A. Tectibranchiata
1. Actaeonidae
2. Ringiculidae
3. Akeratidae
4. Hydatinidae
5. Bullidae
6. Tornatinidae
7. Scaphandridae
8. Philinidae
9. Umbraculidae
B. Pteropoda
1. Limacinidae
2. Cavoliniidae
C. Conularida
1. Tentaculitidae
2. Torellellidae
3. Hyolithidae
4. Conulariidae
Order 2. Pulmonata
A. Thalassophila
B. Basommatophora
1. Auriculidae
2. Chilinidae
3. Physidae
4. Limnaeidae
5. Ancylidae
C. Teletremata
D. Stylommatophora

vicarious. A very different aspect is presented by the Eocene fauna of Australia, New Zealand, and South America, where we find the evident forerunners of forms now inhabiting the southern portions of the Atlantic and Pacific Oceans.

Still more intimate is the relationship existing between the fossil land and fresh-water Gastropods and their descendants on the several continents. It has been observed that Miocene faunas bear a decidedly tropical stamp. On this account European and American forms from the inland Miocene deposits bear some resemblance to the recent faunas of the Azores and the West Indies, as well as to the land and fresh-water Gastropods inhabiting the colder latitudes of Europe and Asia. Only as recently as the Pliocene did each geographical province come to assume its present distinctive features.

In general, the stratigraphic sequence of Gastropod groups corresponds closely with the zoological order, the most generalised forms appearing first, the more specialised later. Beginning with the two-gilled *Rhipidoglossa* and the *Docoglossa*, followed by the single-gilled *Rhipidoglossa*, Opisthobranchs, and taenioglossate Ctenobranchs, the series leads to *Rachiglossa* in the later Mesozoic, and culminates in the great increase of rachiglossate and toxoglossate families in Tertiary and Recent times.[1] (See tables, pp. 500, 501.)

Class 5. CEPHALOPODA.[2]

Head sharply defined in recent forms, except Nautilus. Foot transformed into a

[1] Grateful acknowledgments are due to Professor Henry A. Pilsbry, of the Philadelphia Academy of Natural Sciences, for his revision of the preceding Gastropod chapter. The difficulty of adapting a strictly zoological classification, based largely upon the anatomy of the soft parts, to the practical needs of the palaeontologist, is strikingly illustrated by the class of Gastropods. A revolutionary, or even extreme course has been avoided; and it is hoped that the system herein adopted will be found to possess some practical advantages.—TRANS.]

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funnel-shaped muscular swimming-organ; mouth provided with jaws and radula.

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tacles surround the mouth, and serve as prehensile and locomotive organs; in the Dibranchiates they are armed with hooks and suckers.[1]

The Cephalopods are the most highly organised, and include some of the largest of all the *Mollusca*. They breathe by gills, and are exclusively marine. Their nervous, circulatory, digestive, and reproductive systems, their musculature, and sense organs all exhibit remarkable differentiation as compared with those of other Mollusks. A fleshy mantle, which is open above, encloses the cavity which is occupied by the respiratory organs (the gills), and it also serves as a covering for the reproductive, alimentary, and secretory systems, the heart, and the principal blood-vessels. A large ganglionic mass (cerebral ganglion) and sub-oesophageal ganglion connected by commissures are placed around the oesophagus, and are surrounded by a cartilaginous enclosure in the Dibranchiates, but in *Nautilus* this protects only the sub-oesophageal nerve mass.

Recent Cephalopods were divided by Owen into two groups—*Tetrabranchiata* and *Dibranchiata*. The former is represented in the present fauna by the solitary genus *Nautilus*, but the latter still comprises a very considerable series of forms. A host of fossil Cephalopods abounded in the Palaeozoic and Mesozoic seas. The two largest groups of these, *Ammonoidea* and *Belemnoidea*, do not afford any certain information regarding the number of gills, but the shells of the former agree essentially with those of Nautili, while those of Belemnites, on the other hand, are more like those of certain Dibranchiates; hence it is advisable to associate these fossil groups with the corresponding recent sub-classes.

Sub-Class 1. TETRABRANCHIATA. Owen.[2]

Cephalopods with four plum-like gills, and external, chambered shells. Ambulatory funnel divided; ink-bag absent; arms represented in existing Nautili by lobes

Fossils, vol. III., *ibid.* 1884-97.—Contributions to Canadian Palaeontology, vol. I., 1885-89.—Descriptions of Fossils from the Devonian of Manitoba (Trans. Roy. Soc. Canada, vol. VIII. sec. 4), 1890.—*Whitfield, R. P.*, Several papers in Bull. Amer. Mus. Nat. Hist., especially I., No. 8, 1886; II., No. 2, 1889; III., No. 1, 1890; IX., No. 2, 1897.—Republication of Hall's Fossils, etc. (*ibid.* vol. I., Part II.), 1895.—*Wright, T.*, Monograph on the Lias Ammonites (Palaeont. Soc.), 1878-86.—*Wärtenberger, R.*, Studien über die Stammgeschichte der Ammoniten (Darwinistische Schrifte, No. 5). Leipzic, 1880.—*Zittel, K. A.*, Cephalopoden der Stramberger Schichten (Palaeont. Mittheil. Museum Bayer. Staates, Bd. II.), 1868.—Die Fauna der älteren Tithonbildungen (*ibid.* Bd. III.), 1870.—Handbuch der Palaeontologie, Bd. II., 1881-85.

[1] Professor A. E. Verrill, whose knowledge of existing Cephalopods is not excelled by that of any other malacologist, has kindly furnished the following and some other notes at the request of Professor Hyatt:—

"The arms, together with the siphon (ambulatory funnel) of Cephalopods, must be considered as homologous with the foot of other *Mollusca*. The large nerves supplying these organs arise from the pedal ganglia. In the early larval stages the arms arise as bud-like, paired lateral outgrowths at the base of the large yolk-sac, while the rudiments of the siphon (funnel) arise as two oblique pairs of folds situated further back. The anterior pair of these folds eventually unite and form the central or tubular part of the siphon, and the more posterior folds form the lateral or valvular portions of the same organ. The rudimentary arms arise posterior to the mouth on the ventral and lateral sides of the yolk-sac, and only surround the buccal region at a later stage. The yolk-sac occupies the same relative position, behind the mouth, as the central part of the foot-area of ordinary Gastropod larvae in the early veliger stages. Therefore the arms are muscular, lateral outgrowths of this same foot-area. The two lateral rows of rudimentary arms are widely separated at first by the yolk, but during the absorption of this, they rapidly approach each other and converge around the mouth."

[2] *Owen, R.*, Memoir on the Pearly Nautilus. London, 1832.

and numerous tentacles, which are without hooks and suckers.[1] Cambrian to Recent.

Our knowledge of the soft parts of the Tetrabranchiates is based entirely upon the single existing genus *Nautilus* (Fig. 1049). The animal is contained in the outermost compartment (living chamber) of the shell, the ventral portions being on the external side. The body is short and thick, and the head separated from the remaining portion. Around the mouth are about ninety external filiform tentacles, placed upon the edges of lobes, and their basal parts when contracted are lodged in fleshy sockets or sheaths. The pair of tentacles on the inner or dorsal side are fused so as to form a thicker muscular lobe or hood, which serves to close the aperture of the shell when the animal is withdrawn into the living chamber. On the ventral side of the head and tentacles, but separated from them, is a very thick muscular leaf, having the free edges external and rolled in upon themselves (Fig. 1049, *d*). This is the so-called ambulatory funnel of authors generally (*hyponome* of Hyatt), and its cavity is contracted anteriorly and dilated posteriorly, where it opens into the branchial chamber. It serves to conduct water which is taken by suction into, and then violently expelled from the gill cavity of the mantle, thus driving the creature backward by the force of reaction. Kerr[2] suggests that the structure of the infolding edges of the hyponome and the muscular character of this organ would enable the animal to unroll and flatten it out so as to be available for crawling. It is supposed to be homologous with the foot of Gastropods, and this suggestion, if true, would show that it had not entirely lost its normal functions in primitive forms of *Cephalopoda*.

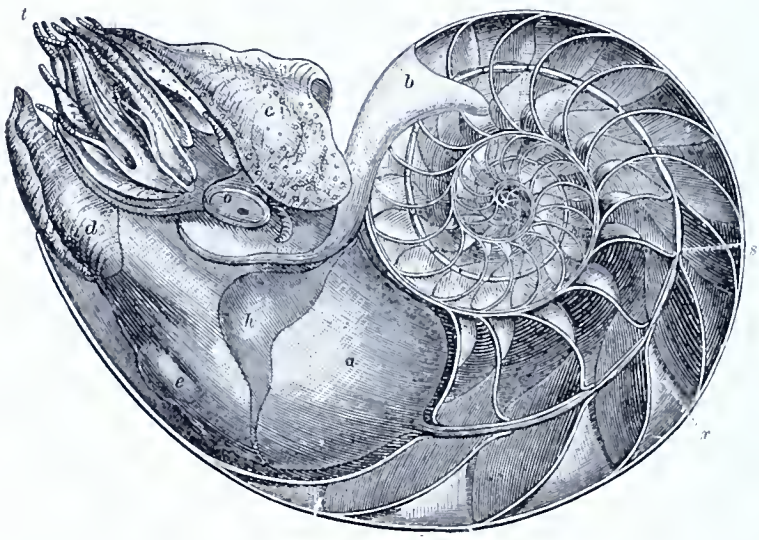


Fig. 1049.

Nautilus pompilius, Linn. Recent; Indian Ocean. Shell with contained animal cut through along the median line. *a*, Mantle; *b*, Dorsal lobe of the mantle; *c*, Hood; *d*, Hyponome, or "ambulatory funnel"; *e*, Nidamental gland; *h*, Muscle for attachment; *o*, Eye; *s*, Siphuncle; *t*, Tentacles; *x*, Septal chamber (after R. Owen).

On either side of the head, near the pair of lateral tentacles, is placed a large eye of primitive structure, which is supported on a short pedunele. The mouth is in the centre of the lobes and groups of tentacles, the tongue is fleshy, and the radula armed with numerous rows of plates and hooks. The remarkably powerful jaws (Figs. 1050, 1051) are largely composed of a dark,

[1] Professor Verrill homologises the lobes of *Nautilus* with the arms of the *Dibranchiata*, and the tentacles with the small lateral tentacles that fringe the arms in a number of deep-sea forms belonging to that sub-class.

[2] *Kerr, J. G.*, Anatomy of Nautilus pompilius (Proc. Zool. Soc., London, pp. 664-686), 1895.

horny substance, only their points being calcified. Similar calcified beaks are not uncommon in Mesozoic terranes, being found either associated with Nautiloid shells or detached. The jaws belonging to *Temnocheilus bidorsatus* from

Fig. 1050.

Upper jaw of *Nautilus pompilius*. *A*, Side view. *B*, Inferior aspect. 1/1.

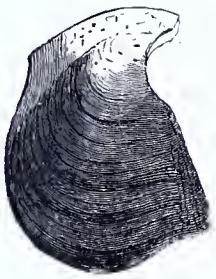


Fig. 1051.

Lower jaw of *Nautilus pompilius*, side view, 1/1.

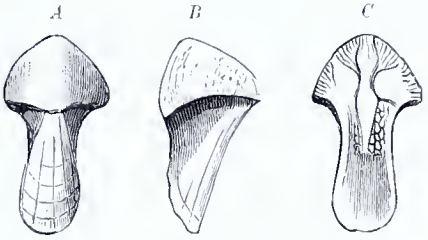


Fig. 1052.

Temnocheilus bidorsatus, Schloth. (=*Rhyncholithes hirundo*, Faure-Biguet). Muschelkalk; Laineck, near Bayreuth. *A*, Upper jaw, viewed from above. *B*, from the side. *C*, from below.

the Trias were originally described under the name of *Rhyncholites* and *Conchorhynchus* (Figs. 1052, 1053); the common Jurassic and Cretaceous forms are known as *Rhynchoteuthis* (Fig. 1054) and *Palaeoteuthis*, d'Orbigny. The long, feather-like gills are disposed in two pairs at the base of the hyponome, and between them is the anus, closely behind which is placed the single or double orifice of the generative organs. In the female there is found at the base of the gill cavity a long, tripartite, nidamental gland, which fuses externally with the mantle.

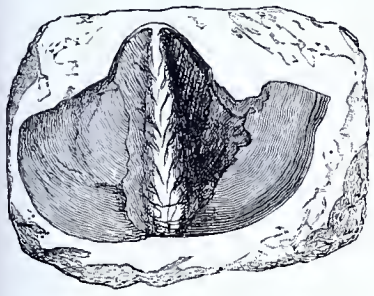


Fig. 1053.

Temnocheilus bidorsatus, Schloth. (=*Conchorhynchus avirostris*, Blainv.). Muschelkalk; Laineck, near Bayreuth. Lower jaw viewed from above.

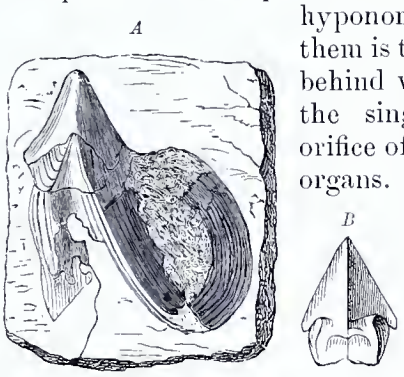


Fig. 1054.

Rhynchoteuthis Sabaudianus, Pict. and Lor. Neocomian; Voirons, France. *A*, Dorsal aspect, showing in part the chitinous lateral expansions. *B*, The calcareous beak seen from below.

The body is short, sack-shaped, rounded posteriorly, and enveloped by the mantle. The base of the latter is prolonged at a certain point into a fleshy, hollow cord or tube (*the siphon*), which passes through a rounded aperture in each of the septa, and extends as far as the inner side of the apex in the initial chamber. The fastening of the animal within the living chamber is accomplished by two oval muscles situated on either side near the base of the mantle. These muscles are attached to the inner wall of the living chamber, and have corresponding, but very shallow impressions. They are connected both dorsally and ventrally by a band of fibres, the *annulus*, which also leaves its impression upon the shell. The form and position of the muscles for attachment and the annulus are sometimes discernible on the casts of fossil shells.

The shells of existing Nautili are coiled in one plane, and composed of

several volutions, the outermost of which either envelopes all the earlier ones (*Nautilus pompilius*), or leaves the umbilicus partly open (*N. umbilicatus*). With the exception of the last half of the outer volution, which is occupied by the animal as a living chamber, the shell is divided up into numerous cavities or chambers by parallel partitions called *septa*, the mesal parts of which are concave toward the aperture; and they are disposed at regular intervals. The compartments thus formed are said by different authors to be filled with air, gaseous, or even fluid matter, and all are traversed by the siphon.[1]

This organ has dense walls and is probably not capable of any extended movements inside of the surrounding calcareous parts which form the siphuncle. The relation of the siphuncle to the septal chambers in *Nautilus* has not been sufficiently investigated to enable one to state distinctly what its functions may be. The whole exterior of the mantle and siphon is encased in a cuticle of horny matter, the remains of which are often found in the living chambers and siphuncles of fossil forms as well. The shell itself is composed of two layers, an internal and an external. The outer layer is composed of imbricated laminae, is porcellanous, light-coloured, and superficially ornamented with red or brown transverse bands; the inner layer is nacreous, and composed of thin, parallel laminae, which are crossed by fine rectangular lines. The septa likewise consist of a pearly layer, but are covered over like the inner walls of the chambers with a very thin, opaque, calcareous film. A large number of fossil shells have a structure similar to the recent *Nautilus*. These are divided into several groups, characterised by peculiarities of the initial chamber, and by differences in the suture lines, siphuncles, sculpturing, and form of the aperture.

Our knowledge of the life-history of the *Nautilus* is very limited. Although empty shells are cast ashore in great quantities in the Pacific and Indian Oceans, the animal is rarely found alive. According to Rumphius, the creature swims by ejecting water through the hyponome, and at the same time holds the tentacles expanded horizontally, and the head protruded as far as possible; but when creeping, probably the head and tentacles are directed downward.[2] The shell is essentially alike in both cases. However, in *Nautilus pompilius*, Willey has found that the females differ in having flatter and more convergent sides, the males being stouter and more gibbous, which is exactly contrary to the prevalent notions with regard to sex among shell-bearing Cephalopods. The shell is supposed to serve as a hydrostatic apparatus, sinking when the animal withdraws into the living chamber, but suffi-

[1] These conditions are described by Professor Verrill in the following note:—"The pericardium of *Nautilus pompilius* communicates directly with the gill cavity by special pores, which are close to the orifices of the nephridia, but do not unite directly with latter, as in most *Mollusca*. Water can, therefore, pass directly into the pericardium and other coelomic cavities. The cavity of the siphuncle appears to communicate directly with the pericardium, and hence with the gill cavity by means of the special pores. Thus sea-water can readily pass into or out from the chambers of the shell, to equalise pressure at varying depths, as in most marine *Mollusca*. These chambers are unquestionably filled with fluid under normal conditions. But living as the animal does under pressure at considerable depths, the fluid in the chambers is saturated with the gases in solution. When the *Nautilus* is rapidly brought to the surface, some of the gas is liberated in consequence of diminished pressure, and must occupy part of the space within the chambers by forcing out some of the fluid. Hence the shell will float until the free gases within the chambers are absorbed or otherwise eliminated. There is no evidence that free gases are ever naturally present in the living chambers during life."

[2] *Rumphius, G. E.*, d'Amboinische Rariteitkamer, p. 59. Amsterdam, 1705.

ciently buoyant to float itself and the animal when the head and tentacles are protruded in the act of swimming. Moseley [1] confirms the observations of Rumphius, but the animal he studied was drawn up by a dredge which had been dragged on the bottom at a depth of 300 fathoms. This individual swam in the manner described, but was not able to sink; and this was accounted for on the supposition that in rising from the bottom the sudden expansion and rarefication of the contents of the air-chambers had interfered with the action of the hydrostatic apparatus.

Nothing has yet been ascertained regarding the mode of reproduction and development of the animal in *Nautilus*. The construction of the shell in this genus, however, renders it probable that in the youngest stage a perishable embryonal shell was formed, the presence of which is indicated by a scar or cicatrix on the apex of the initial chamber. Hyatt describes and figures a more or less wrinkled lump on the apex of several species of the *Orthoceratidae*, which he regards as an embryonal shell or protoconch; and Clarke also figures one having a nearly perfect form. The former explains the absence of the protoconch in most genera and in the recent *Nautilus* by supposing it was usually membraneous or imperfectly calcified, and hence easily destroyed.

As the animal continued to grow, it advanced forward by building out the edges of the aperture and secreted new septa at regular intervals, each one probably corresponding to a period of repose. A tubular prolongation of the base of the mantle was formed at each period of progress, and this remained behind in the first septal chamber and excreted the calcareous matter that built the last segment of the siphuncle. Each septum bends apically into a funnel around the origin of the siphon at the base of the mantle, and this is continuous with a calcareous but more loosely constructed and very porous wall that prolongs the tube begun by the funnel. This porous wall or sheath coats the funnel on its external surface in the air-chambers, but it continues alone apically beyond the funnel, and is inserted into the spreading trumpet-like opening of the next preceding funnel. The siphuncle is therefore a segmented, calcareous tube surrounding the siphon, each segment crossing only one septal chamber and consisting of a funnel and its connecting sheath.[2]

In *Nautilus* the margin of the external opening or aperture is sinuous, the concavities being the sinuses, the outward convexities the crests; and the single, median, concave bend on the venter is named the *hyponomic sinus*, because it indicates the position of the hyponome. In some fossil genera (*Orthoceras*) the aperture is often straight or simple (Fig. 1062); in others the lateral margins are produced in the form of ear-like crests or *lappets* (*Lituites*, *Ophidioceras*); and in some forms they approximate more or less, forming contracted apertures.

The closure of the aperture is never complete, and may take place through the inward growth of the lateral margins, as in *Phragmoceras* (Fig. 1087), forming a direct dorso-ventral slit, or from the venter and the sides, as in

[1] *Moseley, H. N.*, Narrative of the Voyage of the *Challenger*, vol. I. p. 490.—*Fischer, P.*, Manuel de Conchyliologie, p. 473, 1880-87.—*Willey, A.*, In the Home of the Nautilus (Natural Science, vol. VI. p. 411), 1895.

[2] *Brooks, H.*, On the Structure of the Siphon and Funnel in Nautilus pompilius (Proc. Boston Soc. Nat. Hist., vol. XXIII. p. 380), 1888.—*Appelöf, A.*, Die Schalen von Sepia, Spirula und Nautilus (Kon. Svensk. Vetensk. Akad. Handling., vol. XXV. No. 7), 1895.

Dimerites (Fig. 1084), producing a T-shaped opening; or, as in *Hercoceras* (Fig. 1071), it may occur principally from the dorsum and venter, resulting in a transverse aperture. The dorsal side of the aperture is, as a rule, occupied by a crest, known as the dorsal crest (Figs. 1066, 1072, 1089). The position of the hyponome is indicated by the large single opening and sinus at the termination of the longer median slit of the aperture in shells with contracted openings that obviously had this organ (*Phragmoceras*, *Gomphoceras*, etc.); but in others like *Hercoceras*, which have no ventral sinus in the aperture, the hyponome was probably absent or non-functional. The sinus in the lines of growth, however (Fig. 1071), show that this organ was present in the preceding stages of development before the contracted apertures were formed.

Dr. Pompeckj states that contracted apertures occur only in the senile stages of growth, and small shells having this peculiarity must be regarded as dwarfs. This is certainly true of many species, and is probably also the case with *Hercoceras* and the like. T-shaped apertures often show several accessory sinuses and crests (Fig. 1085), which probably indicate the number of their protrusible arms or tentacles. Most curved forms have the ventral sinus on the arched external side (*exogastric* shells), but some have it on the concave internal side, as in *Phragmoceras*, and these are called *endogastric* shells. The interior wall of the living chamber, and volutions in recent and fossil Nautiloids (Fig. 1073), are normally marked with fine transverse and longitudinal lines. In the recent *Nautilus* a black superficial layer, composed in part of organic matter, is deposited by the hood immediately in front of the aperture on the dorsum.

The internal partitions or septa, which divide the volutions into chambers, vary exceedingly in number among different species and also at different ages of the same individual; but they are tolerably constant as a rule, within the limits of one and the same species, if specimens of the same age are compared. They follow one another in regular succession, but as observed by Hyatt, the intervals are relatively greater in the young, more constant in the adult, and then markedly decrease in the oldest stage of development. Each septal chamber (*camera* of Hyatt) was part of the living chamber until it was cut off by a septum and left empty as the animal moved forward. Perfectly preserved shells may have the living chamber alone filled up with stony matrix, since the sediment could only pass into the preceding chambers through the siphuncle, or as a result of injury to the walls of the camerae. Nevertheless, these last are seldom entirely empty, their interiors being frequently lined with crystals of infiltrated calcite, quartz, celestine, baryte, pyrite, or with organic excretions. Double septa occur in some forms (*Actinoceras*), and in others the camerae are sometimes secondarily partitioned off by intermediate walls or pseudo-septa, which may either run parallel with the septa proper, or at an angle with them, and are composed of two readily separable calcareous lamellae. The origin of these pseudo-septa has been attributed to the calcification of regularly arched membranes at the posterior end of the body.

The line of junction between the septa and inner wall of the shell is called the *suture*. This is invisible externally, except when the shell-substance has been broken or worn, or dissolved away, and it is seen most clearly on natural casts. The sutures of Nautiloid shells follow, as a rule, simple, straight, or slightly undulating lines. These undulations, when convex toward the apex, are termed *lobes*, and the reversed or orad curves are the *saddles*. They are

called *lateral lobes* when occurring on the sides, and when on the venter or dorsum are termed *ventral* or *dorsal lobes and saddles.* The *annular lobe* is a small median dorsal lobe, usually pointed and occupying the centre of the main dorsal lobe. It is supposed to have had some relation to the corresponding inflection or point of the annular muscle among the *Nautiloidea.* In more specialised shells it is associated with a conical inflection of the septum itself. The curves are undulatory as a rule, but in some genera may be more or less angular.

The position of the siphuncle does not enable one to determine which is the ventral and which the dorsal side in most genera, but the hyponomic sinus in the aperture and the curved lines of growth are an almost unfailing index of the ventral side. The siphuncle is apt to change its position in the same individual at different stages of growth, but in shells of the same age it is approximately constant, and is available for diagnostic purposes in a number of genera.

The siphuncle is variable in form and characteristics among Palaeozoic genera, being tubular in some (Fig. 1061), or inflated in the interseptal spaces in others, in such manner as to resemble a string of beads, or swollen discs which are separated by narrow constrictions (Fig. 1077). When of considerable width, its cavity is partly filled up with thin calcareous lamellae (Fig. 1088), partly with the calcareous cones immediately to be described (Fig. 1056), or it is notably reduced by excretions around the interior of the funnels forming peculiar annular swellings known as rings, and which are generally composed of calcareous matter. The centre of the siphuncle in these forms is usually kept open more or less perfectly by an axial tube termed by Zittel the *prosiphon* (*endosiphuncle* of Hyatt), which will be considered more fully in the descriptions of *Endoceras* and *Actinoceras.* In *Diphragmoceras* the siphuncle is septate like the shell. The upper parts of these large siphuncles were more or less unobstructed near the living chamber, and this part (the *endoconal* or *siphuncular chamber* of Hyatt) was doubtless occupied by an extension of the mantle cavity, probably containing portions of the viscera.

The funnel of the siphuncle as described above is simple in structure, and is plainly directed towards the apex in all Nautiloids, with the exception of *Nothoceras* and its allies, the funnels (?) of which are turned in the opposite direction. The funnels, as a rule, are short and incomplete, although in the early stages of development of many shells, and in the adult stage of primitive forms they may be complete, extending from one septum to the next following (Fig. 1056), or even to the second preceding this (Fig. 1055, *C*). When the funnels are complete they are always contracted apically, and inserted one within the other. The siphuncle in most Nautiloids, as in the existing *Nautilus* (Fig. 1074), is apt to be more or less dilated in the younger stages, especially in the second and first air-chambers, and it is closed at the end within the first air-chamber by what is termed the *caecum.* The external shell is perforated by an elongated scar or cicatrix (Fig. 1073), closed by a plate, against some part of which the bottom of the caecum impinges in the interior. The presence of the cicatrix, as already stated, leads to the inference that a deciduous embryonal shell or protoconch must have been present. The shell on the apex is so much thinner than at later stages, and is so easily abraded or destroyed, and the cicatrix itself in consequence so slightly marked

even in perfect shells, that good examples are rarely found, and when met with require careful preparation and close observation.

In some Palaeozoic Nautiloids with large siphuncles (*Endoceras*, *Actinoceras*), the apical end of the siphuncle is solid and dilated to form the *nepionic bulb* (Hyatt), and this sometimes practically fills the camerae, and besides being very large in a number of succeeding chambers. The endosiphuncle expands near the apex in these genera, and forms a good-sized conical perforation or cicatrix, which is obviously open at its termination (*Actinoceras*, *Nanno*).

Closely coiled shells have the apical part bent so as to enclose a vacant space (the *umbilical perforation*) in the centre of the whorls (Fig. 1070). This is present in all the *Nautiloidea* having this mode of growth, although in some genera it is very minute. The Nautiloid shell is invariably cone-shaped, but this may be straight or curved, or coiled in open or closed spirals, but in rare instances it is even screw-like, or similar to a Gastropod shell. Along with perfectly smooth shells, or those marked only with fine growth-lines, which in some rare cases may retain traces of their original coloration, there are others with external transverse ridges, keels, rows of tubercles or laminae; but this ornamentation is of a simple kind, and never attains the degree of complexity observed among the more highly ornamented forms of Ammonoids.

Classification.—Great importance has always been attributed to the external configuration and curvature of the shell in distinguishing genera, and the principal groups usually named *Orthoceras*, *Cyrtoceras*, *Gyroceras*, *Nautilus*, etc., have been founded upon such characters. Barrande emphasised in addition the shape of the aperture, direction of the funnels, and structure of the siphuncle, but considered these subordinate in most cases to the general form, and the majority of writers have followed his example. Hyatt, however, has regarded the general form and involution of the shell as relatively minor characters, and depends upon coincidence of structure, outlines of the aperture, and especially resemblances in developmental stages, as surer guides to the affinities of the species and characteristics of the genera.

Terminology.[1]—For sake of convenience, it is preferable always to speak of the embryonal shell as the *protoconch*, and the later or epembryonic stages of the shell as the *conch*, the term "shell" being really applicable to the entire external skeleton inclusive of the protoconch. The history of the individual and its shell can be divided into the following stages and sub-stages:—The *embryo* or protoconch; the *nepionic* stage or infancy, represented by the apical part of the conch; *neanic* stage or adolescent part of the more mature cone; *ephebic* or adult stage of the same; and *gerontic* or senile stage with which it terminates in a complete example.

All of these stages differ materially from each other as a rule, and it is often convenient to divide them into sub-stages, connoted by the prefixes *ana-*, *meta-*, and *para-*. Thus the nepionic can be separated into ananepionic, metanepionic, and paranepionic, and it is often essential to treat the neanic and gerontic stages in the same manner.[2]

[1] [The following terminology, and the descriptions and arrangement of the groups from this point onward have been revised by Professor Alpheus Hyatt; and certain alterations as well as much new matter have been introduced into the translation of the original text with the author's permission.—TRANS.]

[2] For a more extended discussion of terminology that can be advantageously used in descriptions of shells of this class see *Hyatt, A.*, Phylogeny of an Acquired Characteristic (1894), p. 422 *et seq.*

The many different forms of Nautiloid shells may be grouped into a few leading types, as follows :—An *orthocone* is the young of the straight as well as many of the coiled forms. In this, although straight, the bands of growth are broader on the venter than on the dorsum, and there is no hyponomic sinus. A *cyrtocone* is the similar stage which replaces or, as is oftener the case, succeeds this and is curved. Both of these may have crests in the bands of growth, on both the dorsum and venter, thus indicating that the young animal did not possess a large hyponome. An *orthoceracone* is the older stage of a straight form, and is nearly or quite straight on both venter and dorsum ; the bands of growth are approximately equal, but there is usually a hyponomic sinus. *Cyrtoceracones* are shells curved like *Cyrtoceras* on both venter and dorsum. *Gyroceracones* are curved in a loose spiral like *Gyroceras*, the volutions being sometimes in contact, but there is no impressed zone, *i.e.* the venter is not involved by the overgrowth of the dorsum belonging to the next outer whorl.

The *impressed zone* in its primitive form is the longitudinal impression formed in the dorsum by the contact of the whorls. This is divisible into two kinds—the contact furrow, arising and lasting only when the whorls are in contact ; and the dorsal furrow, arising through inheritance in the young before the whorls come in contact. There is also a third modification, which for the present may be called the *persistent dorsal furrow*. This occurs in the free senile whorls of some shells, and is a remnant of the impressed zone. Finally, there is a furrow arising only from contact in the old age of some distorted Ammonoids, and hence may be called the *gerontic contact furrow*. Cyrtoceracones and gyroceracones do not usually have impressed zones, but an exception is furnished by *Cyrtoceras depressum*.

Nautilicones are closely coiled shells having an impressed zone. This may be only a very slight contact furrow, or a hereditary dorsal furrow deepening by growth and involution, as in *Nautilus*. *Torticones* are asymmetrical spirals like those of a Gastropod, either loosely or closely coiled. These may or may not have impressed zones. Among Nautiloids they may be distinguished as *trochoceracones*, etc., according to their form, and among Ammonoids as *turriliticones*, etc., when more precise descriptive terms are required. A special nomenclature is employed in describing the position of the siphuncle, which is of convenience in technical treatises, but may be omitted here. The septal chambers have been termed *camerae* in the sequel, because this avoids any assertion with regard to their contents, such as is implied by "air-chambers" and the like. The less appropriate term "loculus" has been used with the same meaning by Holm.

Order 1. NAUTILOIDEA.

The conchs are camerated orthocones and cyrtocones in the young of primitive forms, becoming cyrtoceracones like the adults of these same ancestral shells in the young of more specialised and coiled shells. Apertures have, as a rule, ventral or hyponomic sinuses, and crests on the dorsum. Septa are concave along the mesal plane towards the apex. Sutures straight or undulated, rarely with sub-angular lobes and saddles, and these are probably never acutely angular, as in the Ammonoidea. Each segment of the siphuncle is composed of funnel and sheath as among primitive Ammonoids, but the funnel persists throughout life in the ontogeny of all forms (except perhaps Nothoceras). Collars around the oral openings of the funnel are present in the later stages of Ascoceras (and Nothoceras ?). Apex cup- or saucer-shaped, and marked by a circular or elongated cavity

or cicatrix, which is more or less compressed elliptical, never transversely elliptical or depressed, and is sometimes hidden by the protoconch or its shrunken remnants.

The order may be subdivided according to the general external features of the shell and structure of the siphuncle into five sub-orders, as follows, named with reference to peculiarities of the funnels :—*Holochoanites*, *Mixochoanites*, *Schistochoanites*, *Orthochoanites*, *Cyrtochoanites*. The characters of these different groups are defined under their proper headings.

Sub-Order A. HOLOCHOANITES. Hyatt.

Funnels of siphuncular segments reaching from the septum of origination to the plane of the next septum apicad or beyond this, or in some genera even to the plane of the second septum.

I. Diphragmida.

This group contains but one family, *Diphragmidae*, having the same characters as the following unique genus :—

Diphragmoceras, Hyatt. Orthoceracones and cyrtoceracones having simple septa and sutures as in *Endoceratida*, but siphuncle divided by tabulae alternating with the septa of the camerated shell. Chambers of siphuncle empty, as are also the camerae. Quebec Group.

II. Endoceratida.

Orthoceracones, cyrtoceracones, gyroceracones, and nautilicones having siphuncles of variable diameter, but as a rule large in proportion to width of the shell. They may be empty or filled with internal organic deposits, but are invariably tubular, and the funnels completely shut off the interior from the interiors of the camerae. The latter are without organic deposits.

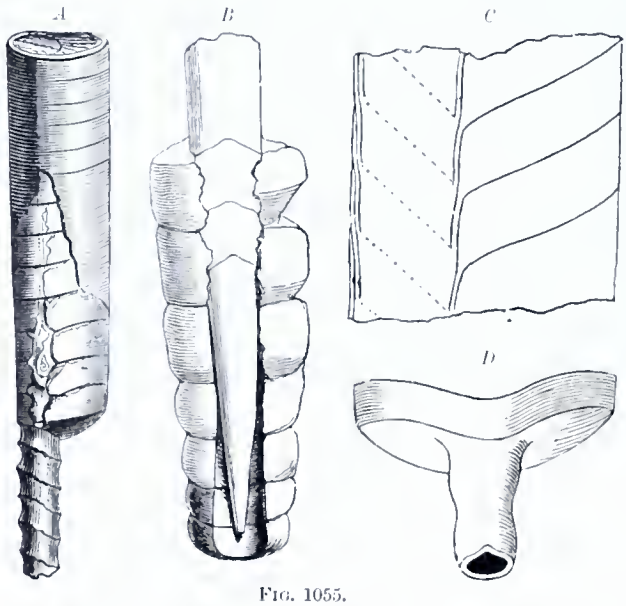


Fig. 1055.

A, *Vaginoceras* (*End.*) *duplex*, Wahlb. Ordovician; Kinnekulle, Sweden. Much reduced. *B*, *V. commune*, Wahlb. Ordovician; Oranienbaum, Russia. The anterior endocone of the siphuncle is filled up with matrix so as to form a dart ("Spiess"). 1/2. *C*, Diagrammatic longitudinal section of the last, showing siphonal funnels. *D*, Detached camera of *Vaginoceras* with long siphonal funnel. (Figs. *C* and *D* after Dewitz.)

Family 1. Endoceratidae.

Smooth or annulated orthoceracones. Siphuncle always more or less filled with organic deposits.

Vaginoceras, Hyatt (Fig. 1055). Ordovician. *Cameroceras*, Conrad (*Sannionites*, Hyatt; *Succoceras*, Holm). Ordovician and Silurian.

Endoceras, Hall (*Colpoceras*, Hall; *Diploceras*, Conrad), (Fig. 1056). Smooth or annulated orthoceracones. Funnels reach from septum of origination to the next apicad of this, but no farther. Septa pass entirely around the siphuncle. Organic deposits in the form of endocones,

and taper off at the centre into a spire that is sometimes tubular and hollow, or again flattened and elliptical. This is the *endosiphuncle*. Ordovician and Silurian.

Narthecoceras, Hyatt. Long, cylindrical, staff-like orthoceracones. Siphuncle large and filled with organic deposits having a radiating fibrous structure like the guard of a Belemnite. Endocones and an endosiphuncle developed. Septa continuous around the siphuncle. Ordovician.

Nanno, Clarke. Similar to the preceding, but endosiphuncle present only at the apical end. Siphuncle close to the shell, so that sutures appear to bend apically into a lobe passing around the siphuncle. Trenton Limestone.

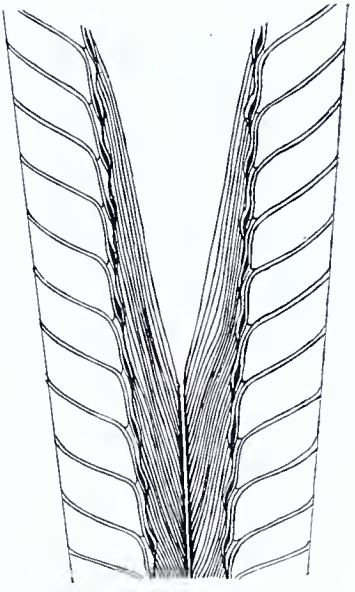


Fig. 1056.

Endoceras proteiforme, Hall. Ordovician; New York. Longitudinal section showing funnels and endocones.

Family 2. Piloceratidae.

Shorter and stouter orthoceracones and cyrtoceracones with relatively larger siphuncles than in Endoceratidae, and more variable in their internal deposits. Septa are more concave and sutures more sinuous. Camerae empty and funnels similar.

Piloceras, Salter. Breviconic cyrtoceracones with very large siphuncle and well-defined endocones. Ordovician.

Family 3. Cyrtendoceratidae.

Gyroceracones and nautilicones having large siphuncles filled with organic deposits or empty, but with endocones obscure or absent, and no endosiphuncles.

Cyrtendoceras, Remelé. Gyroceracones with siphuncle near the dorsum and filled with calcareous deposits. Ordovician.

Sub-Order B. MIXOCHOANITES. Hyatt.

Orthoceracones and cyrtoceracones having expanded living chambers with contracted apertures in the gerontic stage of specialised genera. The oldest septa are bent sharply orad, forming a series of dorsal saddles, and the siphuncle becomes highly modified. Primitive genera have the septa deeply concave or approximately sub-conical, the siphuncle small and empty, and the septa sometimes more or less imperfect on the ventral side in the gerontic stage. Specialised forms have siphuncles with short, straight funnels in the young, and in the ephebic stage collars are built around the oral openings, thus becoming parallel to some forms of Goniatitidae that have similar composite funnels.

Family 1. Ascoceratidae.

Cyrtoceracones, smooth or annulated. Siphuncle with long funnels only in the young and later stages of primitive genera, but collars are added in later stages of specialised forms, and segments become nummuloidal in gerontic stage. Septa often more or less imperfect around siphuncle and on the ventral side.

Choanoceras, Lindstr. Sections depressed elliptical. Gerontic stages have no saddles, and living chamber uncontracted. Ordovician and Silurian.

Aphragmites, Barr. Only gerontic living chambers known; these are similar to those of *Ascoceras*, but have no internal sigmoidal dorsal saddles. Silurian.

Ascoceras, Barr. (Figs. 1057, 1058). Gerontic living chambers internally contracted by the formation of large sigmoidal saddles, and septa more or less incomplete ventrally. Siphuncle with funnels only in the young, the collars in ephebic stages becoming nummuloidal and often incomplete in old age. Aperture open. Silurian.

Glossoceras, Barr. Known only by gerontic living chambers, which are like those of *Ascoceras*, except that aperture has dorsal and lateral crests. Silurian.

Volborthella, Schmidt. Minute orthoceracones with conical septa, small siphuncle, perfectly plain upon the surface of the septa. Living chamber flaring and uncontracted. Lower Cambrian; Finland, Esthonia. St. John's Group; Nova Scotia.

Fig. 1057.

Ascoceras manubrium, Lindström. Silurian; Gottland. $\frac{1}{2}$. (Restored after Lindström.)

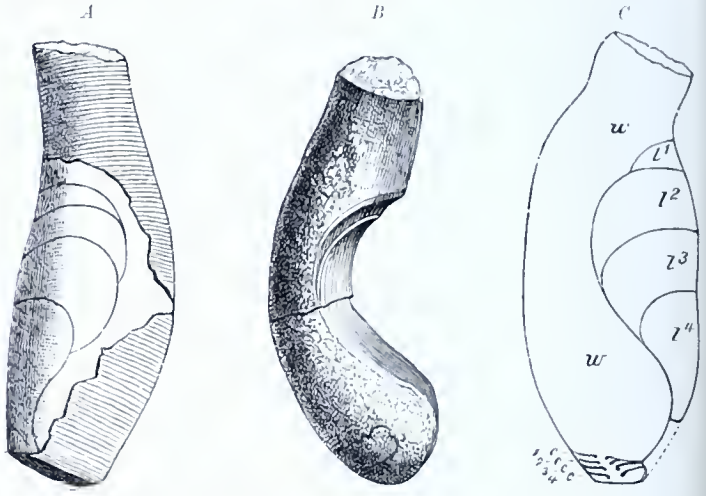


Fig. 1058.

Ascoceras bohemicum, Barr. Silurian (Étage E); Kozorz, Bohemia. *A*, Specimen with shell partially preserved. *B*, Cast of living chamber detached from preceding portion. *C*, Longitudinal section. *w*, Living chamber; *c* 1-4, Camerae; *l* 1-4, Saddles contracting the living chamber. $\frac{1}{1}$ (after Barrande).

Family 2. Mesoceratidae.

Depressed elliptical cyrtoceracones, known only by their gerontic living chambers, and affinities therefore uncertain. They are globular at this stage, and have highly contracted, transversely elongated, and approximately dumb-bell-shaped apertures.

Mesoceras, Barr. Aperture with very shallow hyponomic sinus. No internal gerontic sigmoidal septa. Silurian.

Billingsites, Hyatt. Aperture without hyponomic sinus. Gerontic living chamber partly filled by dorsal sigmoidal saddles as in *Ascoceras*, but septa complete on the ventral side. Silurian.

Sub-Order C. SCHISTOCHOANITES. Hyatt.

Funnels usually more or less imperfect, present on the internal side, and absent or split on the outer side.

This group will be better understood after the publication of Professor W. B.

Dwight's remarkable genera from the Quebec Group near Poughkeepsie, New York. They are probably directly connected with *Holochoanites*. The typical form of the sub-order is, of course, *Conoceras*, Bronn.

Cyrtoceras, Bill. Breviconic cyrtoceracones. Siphuncle large, on the concave side and empty, but having internal ridges alternating with septa of the camerae. These ridges appear to indicate affinity with *Conoceras*. Ordovician.

Conoceras, Bronn (*Bathmoceras*, Barr.), (Fig. 1059). Breviconic orthoceracones, known only in their later stages of development. Siphuncle of moderate size, sub-ventran. Funnels reaching half-way across each camera, steeply inclined orad, and split on the outer side. Closure of the walls effected by a plate extending from the apical opening of each funnel through the funnel itself orad to the apical opening of the next beyond, and projecting into the interior as a flattened fold, which is incomplete or open along the central axis. These internal collars or flat semiconical rings have been described as complete cones (Dwight). Ordovician.

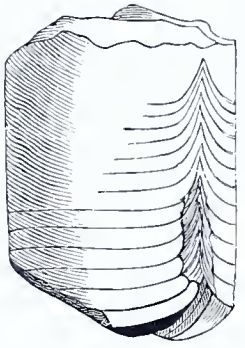


FIG. 1059.

Conoceras praepostorum, Barr. Ordovician (Étage D); Vosek, Bohemia (after Barrande).

Sub-Order D. ORTHOCHOANITES. Hyatt.

Gerontic stages have uncontracted volutions and open apertures, except in a few uncoiled phylogerontic genera. Siphuncular segments may be slightly nummuloidal, fusiform or tubular, but are never markedly nummuloidal, nor are the funnels bent sharply outwards as in Cyrtochoanites. Deposits formed only in the siphuncles of Orthoceratidae and Kionoceras, and in them they are irregular and no endosiphuncles occur; other genera have empty siphuncles. Funnels, as a rule, both longer and straighter than in Cyrtochoanites, and in Aturia almost equal to those of Holochoanites.

This group includes the greater number of Nautiloid forms, passing from the smoothest to the most highly ornamented of Palaeozoic shells, continuing in the Trias as nautilicones of complex ornamentation, and terminating with smooth shells that range from the Jura to the present time. The sutures become more sinuous and complex in one of the subdivisions than in all other Nautiloids. The increase in number of lobes and saddles begins in the Trias with *Clymenonautilus*, and ends with *Aturia* in the Tertiary.

I. ORTHOCERATIDA.

Orthoceracones and cyrtoceracones with smooth or ornamented shells, and not as a rule contracted in gerontic stage; apertures open throughout life. Although often short, none are brevicones, strictly speaking. Section circular or elliptical, very rarely oval. Siphuncle with slightly nummuloidal, fusiform, or tubular segments, and generally near the centre.

Family 1. Orthoceratidae.

Section circular or compressed, living chamber uncontracted or only slightly so, and aperture always open. Surface smooth or with only transverse bands, rarely longitudinal striae, never longitudinal ridges. Siphuncle small (except in Baltoceras), segments fusiform or cylindrical, never nummuloidal. Deposits when present irregular, and gathered about the funnels as in Cyrtochoanites; no definite endosiphuncles ever formed.

Baltoceras, Holm. Siphuncle large, but with short, straight funnels, and sheaths as in *Orthoceras*. Ordovician.

Orthoceras, Breyn (Figs. 1060, 1061). Long tapering orthoceracones and cyrto-

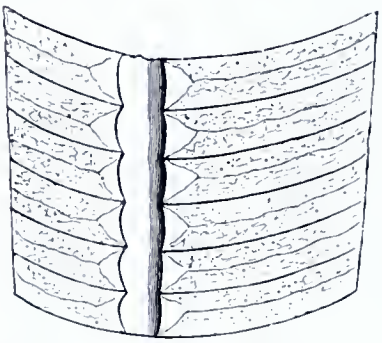


Fig. 1060.

Orthoceras intermedium, Marklin. Silurian; Gottland. Longitudinal section showing siphuncle, septa, and pseudosepta; camerae filled up with calcite.

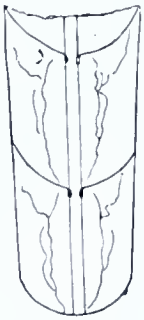


Fig. 1061.

Orthoceras Michelini, Barr. Silurian; Kozorz, Bohemia. Longitudinal section showing short siphonal funnels.

ceracones, smooth, or with only transverse striae and growth bands. Siphuncle generally larger than in *Geisonoceras*, centren or slightly dorsad of centre. Deposits when present gathered about the funnels as in *Annulosiphonata*. Silurian to Trias.

Fig. 1062.

Geisonoceras timidum, Barr. sp. Silurian; Lochkow, Bohemia.

Geisonoceras, Hyatt (Fig. 1062). Similar to the last, but sides spreading more rapidly, and siphuncle empty, centren, or slightly ventrad of centre. Ordovician to Carboniferous.

Fig. 1063.

Dawsonoceras annulatum, Sowb. sp. Silurian (E); Viscocilka, Bohemia. Terminal portion showing shell of living chamber and sectioned camerae (after Barrande).

Protobactrites, gen. nov. Long pencil-shaped orthoceracones and cyrtoceracones, circular or compressed elliptical in section, ornamented with transverse and sometimes longitudinal striae. Siphuncle tubular, centren or near the centre. Truncation occurs in some species, and others are more or less transitional to *Bactrites* among the Ammonoids. Type *P.* (*Orth.*) *styloideum*, Barr. sp. Silurian to Carboniferous.

Family 2. **Cycloceratidae.**

Orthoceracones and cyrtoceracones having annuli with transverse striae or bands of growth at all stages; longitudinal ridges, when present, more or less discontinuous. The earliest forms often have large siphuncles, and are apparently more directly connected with primitive Endoceratida than with Orthoceratidae.

Protocycloceras, gen. nov. Annulated orthoceracones and cyrtoceracones without longitudinal ridges. Siphuncle large. Type *P.* (*Orth.*) *Lamarcki*, Bill. sp. Ordovician.

Cycloceras, M'Coy (*Dictyoceras*, *Heloceras*, Eichw.). Annulated orthoceracones and cyrtoceracones with discontinuous longitudinal ridges. Siphuncle generally tubular or with fusiform segments; deposits when present irregular as in *Orthoceras*. Annuli often become obsolete in parageronic stages. Ordovician to Permian.

Dawsonoceras, Hyatt (Fig. 1063). Similar to *Cycloceras*, but having prominent frilled bands of growth between and on the annulations, the frills

sometimes forming more or less discontinuous longitudinal ridges. Silurian and Devonian.

Ctenoceras, Noetl. Cyrtoceracones like *Dawsonoceras dulce*, Barr. sp., but with fine longitudinal ridges between the annuli, and living chamber with three internal folds or processes—one median dorsan, and a pair on the venter. Siphuncle dorsad of centre. Ordovician.

Family 3. **Kionoceratidae.**

Orthoceracones and cyrtoceracones with more or less well-marked continuous longitudinal ridges, and either with or without annulations. Spinous processes or tubercles often appear at the intersections of the longitudinal and transverse bands of growth. Siphuncle with faintly nummuloidal, fusiform, or tubular segments.

Kionoceras, Hyatt. Longitudinal ridges present as a rule only in the earlier stages, after which inconspicuous annuli appear, but with some few exceptions become obsolete before the ephebic stage. Silurian to Carboniferous.

Spyroceras, Hyatt. Very long, slender, annulated shells, with more or less prominent longitudinal ridges in the ephebic stage. Ordovician to Carboniferous.

Thoracoceras, Eichw. (*Melia*, Eichw.), (Fig. 1064). Like the last, but with more or less spinous longitudinal ridges. Silurian to Carboniferous.

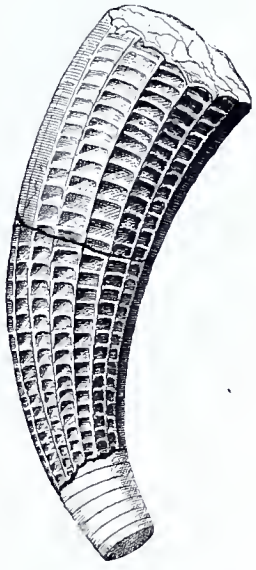


Fig. 1064.

Thoracoceras corbulatum, Barr. sp. Silurian (Étage E); Dvoretz, Bohemia (after Barrande).

II. Plectoceratida.

Orthoceracones, gyroceraconcs, and very discoidal nautilicones with comparatively slight impressed zone. Volutions of gerontic stage often have a centrifugal tendency, becoming sometimes straight and even bending slightly in the opposite or ventral direction. Shells annulated or costated, and often with longitudinal striae or fine ridges, especially in the young, but these generally disappear before the ephebic stage. Siphuncular segments slightly nummuloidal, fusiform, or tubular.

Family 4. **Tarphyceratidae.**

Orthoceracones, cyrtoceracones, gyroceraconcs, and nautilicones, compressed oval in section, venter narrower than the dorsum. Shell smooth or sometimes with primitive fold-like costae. Siphuncle empty, tubular and ventrad of centre.

Aphetoceras, *Deltoceras*, *Barrandeoceras*, *Tarphyceras*, Hyatt; *Planctoceras*, *Eurystomites*, Schröder; *Falcilituites*, Remelé. Ordovician. (For descriptions see Hyatt's *Phylogeny*, 1894.) *Eurystomites* and *Tarphyceras* are wholly nautilicones, the remaining genera either cyrtoceracones or gyroceracones. Orthoceracones represented by genera at present undescribed.

Family 5. **Trocholitidae.**

Nautilicones resembling those of the preceding family, and not easily distinguished from them in the young. As a rule they have excessively broad volutions with reniform section and an impressed zone at a very early age; the siphuncle is then ventrad of the centre, but in the ephebic stage it is tubular and dorsad of centre.

Schroederoceras, *Litoceras*, *Trocholitoceras*, Hyatt; *Trocholites*, Conrad (*Palaconautilus*, *Palaeoclymenia*, Remelé). Ordovician. *Discoceras*, Barrande. Ordovician and Silurian.

Family 6. Plectoceratidae.

Gyroceracones, nautilicones, and torticones having annular costae from the neanic stage until late in life, and in some genera, more or less prominent longitudinal ridges, which usually disappear in the ephebic stage. Siphuncle ventrad of centre.

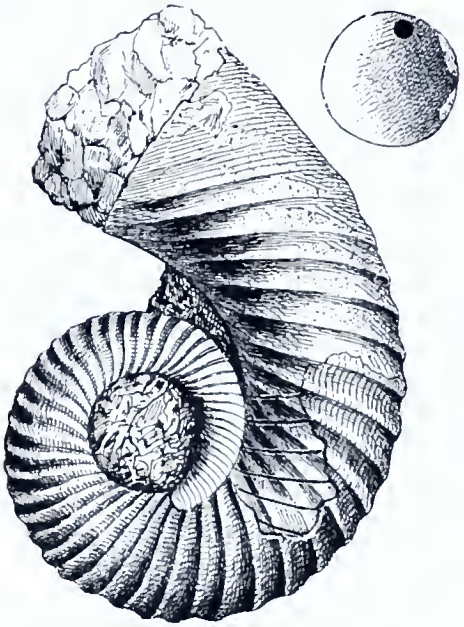


Fig. 1065.

Sphyradoceras optatum, Barr. sp. Silurian (Étage E); Lochkow, Bohemia (after Barrande).

Plectoceras, Hyatt. Ordovician and Silurian. *Sphyradoceras*, Hyatt (*Peismoceras*, *Systrophoceras*, Hyatt), (Fig. 1065). Silurian and Devonian. The first is gyroceraconic, with some discoidal nautilicones, and the second is almost exclusively torticonic of the trochoceran type.

Family 7. Ophidioceratidae.

Discoidal nautilicones, costated from the neanic stage onward. Volutions of the young small and numerous. Section during ephebic stage generally compressed, venter narrower than the dorsum. Siphuncle tubular, small.

Fig. 1066.

Ophidioceras simplex, Barr. Silurian (E); Lochkow, Bohemia. 1/1 (after Barrande).

Ophidioceras, Barr. (Fig. 1066). Nautilicones with straight lateral costae and raised bands on the venter, and longitudinal ridges in the young. Siphuncle dorsad or ventrad of centre during ephebic stage, but ventrad during nepionic. Gerontic apertures with prominent dorsal and lateral crests, and very deep hyponomic sinus. Silurian.

Homaloceras, Whiteaves. Cyrtoceracones with section similar to that of *Ophidioceras*, venter narrow and channeled, bordered by crenulated ridges; the dorsum gibbous and rounded. Siphuncle near the venter. Devonian.

Family 8. Lituitidae.

Excepting the supposed ancestral, primitive genus, Cyclolituites, this is a series of phylogerontic uncoiled forms with an extreme modification in the almost completely uncoiled Rhynchorthoceras. Apertures quite distinct from those of the preceding family; hyponomic sinus shallower, there are narrow ventro-lateral crests, and small lateral sinuses and

Fig. 1067.

Lituites lituus, Montf. Ordovician drift; East Prussia. 1/2 (after Noetling).

crests, some forms having altogether as many as five sinuses and five crests. Siphuncle tubular and usually large.

Cyclolituites, Remelé; *Lituites*, Breyn (Fig. 1067); *Angelinoceras*, *Holmiceras*, Hyatt. Ordovician. *Ancistroceras*, Boll; *Rhynchorthoceras*, Remelé. Ordovician and Silurian. (For re-descriptions see Hyatt's *Phylogeny*, 1894.)

III. Pleuronautilida.

Comparatively smooth nautilicones, the primitive genera discoidal but leading up to some highly involute shells in the Trias. The later Mesozoic and Tertiary shells nearly all deeply involute. Some of the Triassic Clydonautilidae have more sinuous sutures and a greater number of lobes and saddles than any other Nautiloids, and this complexity persists, although to a lesser degree, among the Jurassic, Cretaceous, and Tertiary forms. Siphuncle tubular and small, with mostly short funnels except in Aturia, where they are very long.

Family 9. Grypoceratidae.

Primitive forms have discoidal volutions with very simple sutures, but are succeeded by involute shells having more complex sutures. The latter have prominent ventral saddles sometimes divided by a lobe, and large lateral and dorsal lobes. All genera save one known to have annular lobes. Shells less highly ornamented than in preceding family, and sutures simpler than in the next following.

Syringoceras, Hyatt. Discoidal with primitive, approximately tubular, or slightly compressed volutions. Surface marked by longitudinal ridges, sometimes intersecting the transverse lines so as to produce a cancellated surface. Sutures with faint ventral saddles, slight lateral and dorsal, and minute annular lobes. Siphuncle very small and near the venter. Trias.

Grypoceras, Hyatt. Volutions more or less deeply involved, but umbilicus open, the venter narrow and often channeled. Sutures with narrow, sometimes deep ventral lobe, broad, sweeping lateral lobes, and deep dorsal with annular lobes. Siphuncle dorsad of centre. Trias.

Family 10. Clydonautilidae.

Shells have folds in some species, and all are deeply involute except the primitive genus Clymenonautilus. Lateral lobes of sutures more or less deep and often sub-angular, suggestive of the Clymenidae among Ammonoids. Some highly specialised and involute species have the umbilical lobes exposed on the sides, and an additional pair of laterals developed near the venter, thus making three pairs of lobes on each side. The compressed volutions, narrow venter, and aspect of the young and primitive forms seem to indicate close affinity with the Grypoceratidae, but only a few species of late Mesozoic time are known to have annular lobes.

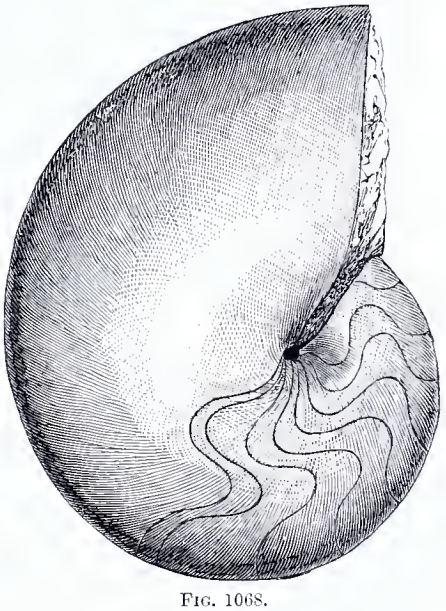


Fig. 1068.

Hercoglossa franconicus, Oppel. sp. Upper Jura; Staffelstein, Franconia.

Clymenonautilus, gen. nov. Smooth, discoidal shells with more or less compressed volutions, and narrow convex venter. Sutures with prominent ventral saddles, one pair of deep lateral lobes, and large marginal saddles. Siphuncle supposed to be near the venter. Type *C.* (*Naut.*) *Ehrlichi*, Mojs. sp. Trias.

Clydonautilus, Mojs. Deeply involved nautilicones with compressed volutions,

narrow concave venter, and umbilicus small or closed. Sutures with prominent ventral saddles undivided by ventral lobes in adult shells. Trias.

Fig. 1069.

Aturia Aturi, Bast. sp. Miocene; Bordeaux. Shell broken open to show siphonal funnels.

Hercoglossa, Conrad (*Enclimatoceras*, Hyatt), (Fig. 1068). Deeply involute, with sutures like those in *Glyphioceratidae*, but the ventral saddle not divided by even the shallow lobe usually found in that family. Annular lobes present only in some species. Siphuncle small, centren or dorsad of centre. Trias to Tertiary.

Pseudonautilus, Meek. Similar to *Hercoglossa*, but with lobes on the venter, and two saddles on either side. Large annular lobes present. Jura.

Aturia, Bronn (Fig. 1069). Similar to *Hercoglossa*, but with large siphuncle close to the dorsum from an early stage onward, and funnels very long and larger than in any genus of Mesozoic or Tertiary Nautiloids. Eocene and Miocene.

IV. Ryticeratida.

Cyrtoceracones, gyroceraeones, and nautilicones having shells covered with more or less projecting bands of growth which often become sinuous or develop into spout-like, spinous, or nodose prominences. In the more specialised shells these are apt to be confined to the venter. The frills in the bands often form coarse longitudinal ridges. Siphuncle tubular or slightly nummuloidal, and commonly ventrad of centre.

Family 11. **Halloceratidae.**

Orthoceracones and cyrtoceraeones having depressed elliptical or subtrigonal sections, venter broader than the dorsum. Shell with closely set and frilled projecting bands of growth, having large ring-like bands at intervals that sometimes expand so as to form wide collars. The highly specialised nautilicones may have a row of large nodes on either side springing from the bases of large spout-like spines. Siphuncle tubular, small, and near the venter.

Zittelloceras, Hyatt. Cyrtoceracones of depressed elliptical section, the venter narrower and more gibbous than the dorsum. The layers finely frilled and closely set in the intervals between more prominent annular bands. Ordovician to Devonian.

Halloceras, Hyatt. Gyroceracones of sub-trigonal section, the venter broad and dorsum sub-angular, with one row of large nodes at each of the ventro-lateral angles. Devonian.

Family 12. **Ryticeratidae.**

Cyrtoceracones and gyroceraeones resembling Halloceratidae, but much larger, with coarser crenulated bands, and often with rows of spout-like spinous processes which sometimes form coarse longitudinal ridges. Siphuncle more or less nummuloidal, and larger than in Halloceratidae.

Ryticeras, Hyatt (*Rutoceras*, Hyatt), *Cophinoceras*, *Strophiceras*, Hyatt. Devonian.

V. Rhadinoceratida.

Cyrtoceracones, gyroceraeones, and nautilicones having smooth or spinous longitudinal ridges in the young, which become large and fluted in some genera, but disappear in others. Ridges more or less sporadically combined with fold-like annulations, thus suggesting direct descent from the Kionoceratidae.

Family 13. **Rhadinoceratidae.**

Primitive discoidal gyroceracones and nautiliconcs with stout volutions, circular or depressed elliptical in section, but becoming reniform in later stages of nautilicones. Shells with longitudinal ridges and sometimes annular folds in the young, but often smooth in ephebic stage. Sutures with ventral, lateral, and dorsal lobes, or almost straight. Siphuncle nummuloidal and often dorsad of centre. Annular lobes known to be present in specialised forms.

Rhadinoceras, *Nephriticeras*, Hyatt. Devonian.

Family 14. **Trigonoceratidae.**

Gyroceracones and nautilicones having at some stage or throughout life trigonal volutions, a more or less concave venter, and generally fluted shell. Sutures with ventral saddles in the young, becoming divided by shallow lobes in later stages, and in some genera the dorsal lobes of the young become divided subsequently by dorsal saddles. Gerontic living chamber occasionally free near the aperture. Annular lobes observed in only one species (Aphelceras disciforme). Young have longitudinal ridges roughened by transverse bands as in Thoracoceras. Siphuncle small, ventrad of centre.

Trigonoceras, M'Coy; *Coelonautilus*, Foord (*Trematodiscus*, Meek; *Trematoceras*, Hyatt); *Subclymenia*, d'Orb.; *Stroboceras*, *Apheleceras*, *Diorugoceras*, *Ephippioceras*, Hyatt. Carboniferous. All nautilicones but the first, which is gyroceraconic.

Family 15. **Triboloceratidae.**

Gyroceracones and nautiliconcs similar to Trigonoceratidae, and with concave venter at an early stage or until late in life. The venter afterwards becomes more or less elevated, and in most species convex. Sutures also similar, but annular lobes are present in all the nautilicones save Coloceras.

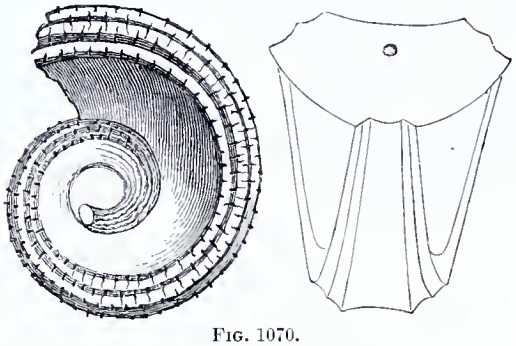


Fig. 1070.

Vestinautilus Koninckii, d'Orb. sp. Carboniferous Limestone; Tournay, Belgium. Oral and lateral aspects of young individual, with umbilical perforation.

Triboloceras, Hyatt; *Vestinautilus*, Rvckh. (Fig. 1070); *Planctoceras*, *Stearoceras*, *Coloceras*, Hyatt. Carboniferous.

Family 16. **Rhineceratidae.**

Gyroceracones and nautiliconcs like Thoracoceras in nepionic stage, but subsequently becoming biangular in section, and generally developing solid, more or less tetragonal volutions. Longitudinal ridges and flutes also developed, but more uniform in size than in the preceding family, and venter always convex. Annular lobes present in all nautilicones so far as known.

Rhineceras, *Lispoceras*, *Thrincoceras*, *Phloioceras*, *Discitoceras* (*Discites*, M'Coy), *Leuroceras*, *Phacoceras*, Hyatt. Carboniferous.

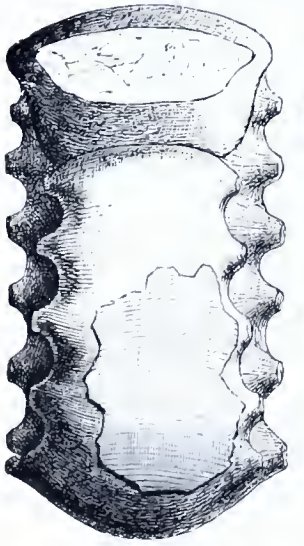
VI. Hercoceratida.

Primitive shells have projecting bands of growth and processes similar to those of primitive Ryticeratida, but less numerous, being present in only one row, and evolving

more rapidly into nodose or symmetrical, spout-like, spinous processes. More specialised forms are tuberculated as in Ryticeratida, but there are never more than three rows of nodes on either side, and these are regularly distributed—one on the umbilical shoulder, another on the ventro-lateral angle, and the third close to the median ventral line. Annular lobes absent except in a few Triassic forms. Siphuncle generally more or less nummuloidal.

Family 17. **Hercoceratidae.**

Cyrtoceracones, gyroceracones, nautilicones, and torticones having depressed elliptical, sub-quadrate, or trapezoidal sections. Aperture has two deep sinuses with projecting edges at the ventro-lateral angles, and these are usually persistent, forming two lines of more or less spout-like processes. Sutures with ventral, lateral, and dorsal lobes. Siphuncle ventrad of centre.



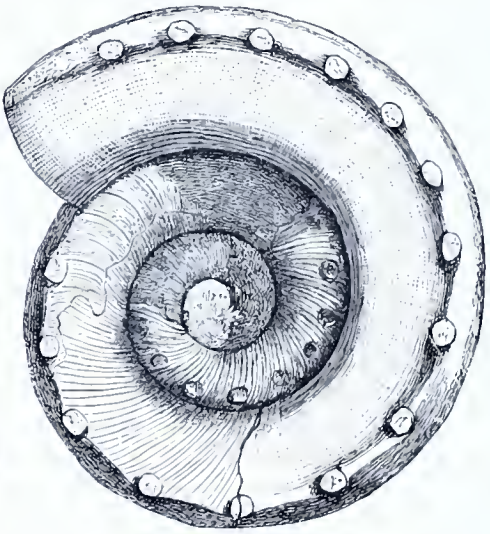


Fig. 1071.

Hercoceras mirum, Barr. Silurian (Étage G); Hlubocep, Bohemia (after Barrande).

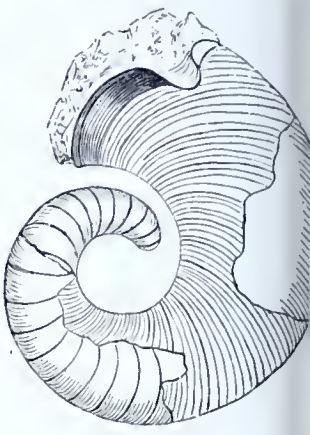


Fig. 1072.

Ptenoceras (*Gyr.*) *alatum*, Barr. sp. Silurian (F); Konieprus, Bohemia. 1/1 (after Barrande).

Hercoceras, Barr. (Fig. 1071); *Trochoceras*, Barr.; *Ptyssoceras*, *Ptenoceras* (Fig. 1072), *Anomaloceras*, Hyatt. Silurian.

Family 18. **Tainoceratidae.**

Discoidal nautilicones with more or less massive volutions which at some stage or throughout life are trapezoidal in section, tuberculated, and without well-defined lateral and umbilical zones. Sutures have ventral, lateral, and dorsal, but no annular lobes. Spinous processes are complete, never spout-like. Siphuncle small, tubular.

Temnocheilus, M'Coy (*Endolobus*, Meek; *Cryptoceras*, d'Orb.). Section trapezoidal throughout life, and one row of persistent spines and nodes on either side at the ventro-lateral angles. Devonian to Carboniferous.

Foordiceras, Hyatt. Permian. *Metacoceras*, *Coelogasteroceras*, Hyatt. Carboniferous. *Diadiploceras*, Hyatt. Devonian. *Tainoceras*, Hyatt. Carboniferous.

Family 19. **Centroceratidae.**

Gyroceracones and nautilicones with young similar to early stages of Temnocheilus before the impressed zone is formed. Shell subsequently becoming tetragonal in section,

the venter flattened or concave, and dorsum remaining convex until a late stage. Nautilicones have a persistent convex centran area in the impressed zone. No annular lobes known.

Centroceras, Hyatt. Devonian to Carboniferous. *Tetragonoceras*, Whiteaves. Devonian.

Family 20. **Pleuronautilidae.**

More or less discoidal nautilicones with stout volutions and large umbilical perforations; the young, especially in primitive species, remaining cyrtoceraeones until a late stage. More specialised shells are costated and tuberculated on the sides. Sutures have annular lobes except in Pselioceras. Siphuncle ventrad of centre in the young, but becoming dorsad in later stages.

Pselioceras, Hyatt. Permian. *Pleuronautilus*, Mojs.; *Eucoiloceras*, gen. nov. Type *E.* (*Pleur.*) *superbus*, Mojs. sp.; *Enoploceras*, gen. nov. Type *E.* (*Naut.*) *Wulfeni*, Mojs. sp.; *Anoploceras*, gen. nov. Type *A.* (*Pleur.*) *ampezzanus*, Mojs. sp. Trias.

VII. Koninckoceratida.

Nautilicones with biangular sections at an early stage of growth, developing later into modified trapezoidal outlines as in many of the Hercoceratida, but shells are smooth, and the trapezoidal form as a rule evolves during the phylogeny into quadrangular, and finally into involute coils with compressed sections, or may become simply more or less trigonal through elevation of the venter. Annular lobes present in most genera. Aperture constantly open, and in some forms remarkable lateral projections are developed during the gerontic stage.

Family 21. **Koninckoceratidae.**

Shells of primitive forms similar to Temnocheilus, but leading into those with tetragonal sections, and finally into highly compressed volutions. All are smooth and have marked umbilical saddles. Volutions with broad umbilical zones which become lateral in the more involute species. Siphuncle ventrad of centre.

Koninckoceras, *Domatoceras*, Hyatt. Carboniferous. *Potoceras*, Hyatt. Devonian (?). *Stenopoceras*, *Peripetoceras*, Hyatt. Permian.

Family 22. **Solenocheilidae.**

Compressed elliptical in section during early stages, but full-grown of primitive forms and young of specialised derivatives have a more or less trigonal section in neanic stage. Later this stock evolves shells with volutions having depressed elliptical or broadly hemispherical outlines. Sutures generally have large ventral saddles, and saddles on the umbilical shoulders. Umbilical zone very broad, the increase by growth of the dorsum being remarkably rapid. Shells smooth, but aperture in gerontic stage may develop peculiar lateral projections, especially at the umbilical shoulders, which are usually very prominent. Siphuncle sub-ventran.

Aipoceras, *Oncodoceras*, Hyatt; *Asymptoceras*, Ryckholt; *Solenocheilus*, Meek. Carboniferous. *Pteronautilus*, Meek. Permian.

Acanthonautilus, Foord. Nautilicones with sub-hemispherical volutions, the dorsum flattened or concave. Aperture developing laterally into two projecting spines at the umbilical shoulders. Carboniferous.

VIII. Digonioceratida.

Primitive forms constantly retain depressed volutions having a more or less biangular or sub-trigonal section; specialised shells repeat these stages in the young, but subsequently become more involute, and the sections change to reniform, sub-quadrangular, or sub-elliptical. Shells smooth except in the single genus Cymatoceras. Aperture simple and open at all stages; gerontic living chamber only slightly contracted.

Family 23. **Estonioceratidae.**

Gyroceracones and discoidal nautilicones having slightly depressed, broad, rapidly increasing biangular sections in the young, but becoming depressed oval or depressed sub-trigonal in later stages. Siphuncle variable in position.

Estoniocceras, Noetl. Ordovician. *Edaphoceras*, *Remeleoceras*, *Lophoceras*, Hyatt; *Diodoceras*, gen. nov. Type *D.* (*End.*) *avonensis*, Dawson sp. Carboniferous. *Digonioceras*, Hyatt. Jura.

Family 24. **Nautilidae.**

Nautilicones with more or less involved volutions, the siphuncle slightly nummuloidal and variable in position, but never near either dorsum or venter except in the young, when it is frequently either near the dorsum or centren. Biangular stage much abbreviated or absent, the trigonal stage present in most shells for a more or less prolonged period, but developing invariably by spreading of the venter into tetragonal, reniform, or hemispherical outlines. Never decidedly discoidal, although umbilicus is often open. More specialised forms have a minute umbilicus, and in some cases it is completely hidden during the ephebic stage, although invariably open in the young. Zone of impression present on the dorsum before the whorls are in contact. Annular lobes often developed at an early stage, but liable to disappear in the adult; absent in some Tertiary species.

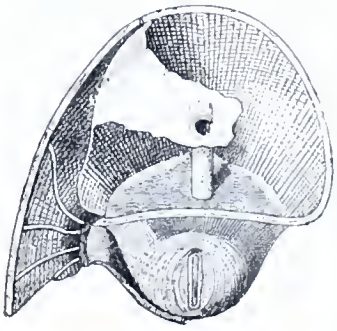


Fig. 1073.

Nautilus pompilius, Linn. Recent. Protoconch showing linear cicatrix at apical end (after Hyatt).

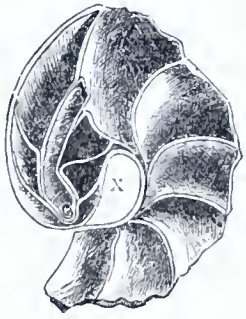


Fig. 1074.

Apical chamber and first volution of *N. pompilius*, sectioned longitudinally. *s*, Siphuncle; *c*, Blind origin of caecum; *x*, Empty space or umbilical perforation (after Branco).

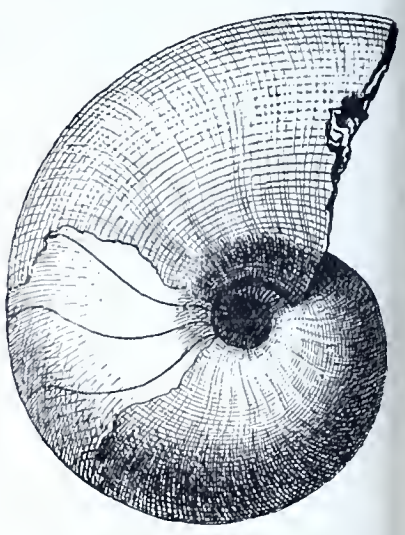


Fig. 1075.

Nautilus intermedius, Sowb. Middle Lias; Hinterweiler, Würtemberg.

Cenoceras, Hyatt. Jura. *Cymatoceras*, Hyatt. Cretaceous. *Eutrephoceras*, Hyatt. Cretaceous and Tertiary.

Nautilus, Linn. (Figs. 1073-1076). The young resembling adults of *Digonioceras* until a late stage, and adults of primitive species (like *N. umbilicatus*) similar to

Cenoceras. Sutures slightly inflected, with faint ventral lobes; annular lobes present. Volutions sub-globose, and umbilical perforation comparatively large. Siphuncle centren in the apical camera, but later becoming ventrad of centre. Tertiary (?) to Recent.

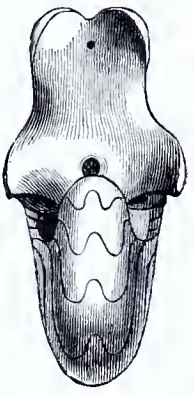


Fig. 1076.

Nautilus Geinitzi. Pictet. Tithonian; Stramberg, Moravia.

Sub-Order E. CYRTOCHOANITES. Hyatt.

Shells varying from orthoceracones to nautilicones, none of them highly ornamented, although some are annulated or costated, and in rare cases slightly nodose. Sutures as a rule simpler than in Orthochoanites. Siphuncle varies exceedingly, passing from tubular in the young and even in the full-grown of primitive forms to highly nummuloidal in the adults of specialised genera, or again in some groups retaining constantly its primitive character. The funnels, however, are as a rule bent outward or crumpled, and generally short.

I. Annulosiphonata.

Mostly orthoceracones and cyrtoceracones, with a few gyroceracones and very rarely nautilicones, the last-named being invariably discoidal. Apertures constantly open. Siphuncle may be empty, but organic deposits when present always gathered about or encrusting the funnels as hollow or solid internal rings. Deposits sometimes sufficient to form more or less annulated endosiphuncles, the rings being opposite the camerae, alternating with the septa, and extending outwardly.

Family 1. Loxoceratidae.

Smooth orthoceracones and cyrtoceracones similar to Orthoceratidae, but siphuncle distinctly nummuloidal, and funnels very short and crumpled. Deposits not uncommon, but irregular, and only irregular endosiphuncles occasionally formed.

Loxoceras, M'Coy (*Sactoceras*, Hyatt). Mostly orthoceracones, circular or elliptical in section. Siphuncle supposed to be tubular in the young, but highly nummuloidal in later stages, centren or near the centre. Septa invariably single, and camerae empty. Ordovician to Carboniferous.

Campyloceras, M'Coy (*Aploceras*, Hyatt). Breviconic cyrtoceracones or orthoceracones with smooth or finely ridged shells, circular or depressed elliptical in section. Siphuncle centren or ventrad of centre. Carboniferous.

Family 2. Uranoceratidae.

Cyrtoceracones, gyroceracones, and nautilicones with stout volutions. Siphuncle in primitive forms highly nummuloidal, but invariably empty; in nautilicones it has less nummuloidal segments, and is uniformly ventrad of centre, but not near the venter. Sutures with ventral saddles, lateral lobes, and also dorsal saddles in primitive forms as well as the young of all shells. Ventral and dorsal lobes arise subsequently in the ontogeny of nautilicones.

Uranoceras, Hyatt. Stout, more or less breviconic cyrtoceracones, compressed elliptical or sub-quadrangular in section. Sutures with broad ventral saddles, lateral and dorsal lobes. Siphuncle large, nummuloidal, centren or ventrad of centre. Devonian and Carboniferous.

Gigantoceras, gen. nov. Gyroceracones similar to the preceding, but having longer living chambers and more compressed volutions. Includes the largest known Nautiloid shells. Type *G.* (*Gyroc.*) *inelegans*, Meek sp. Silurian.

Family 3. Actinoceratidae.

Orthoceracones and cyrtoceracones with siphuncle more or less filled by rings of organic deposits, and having an endosiphuncle in the central axis. Camerae may be empty or filled to various degrees with organic deposits, even to the extent of solidifying the entire shell previous to gerontic stage. Shells smooth or annulated, but not longitudinally ridged, at least in the later stages.

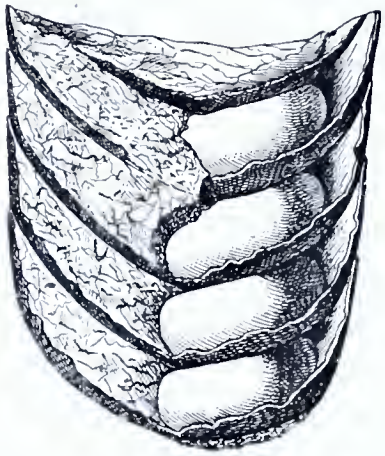


Fig. 1077.

Actinoceras cochleatum, Schloth. Silurian; Gottland. Abraded fragment showing single septa and thick, annulated endosiphuncle. 1/2.

Actinoceras, Bromn. (Figs. 1077, 1078). Orthoceracones and cyrtoceracones of usually depressed elliptical section, with large, excessively nummuloidal siphuncle. Funnels very short and crumpled, sheath almost globular. Internal deposits contracting the central axis into an annulated endosiphuncle with tubuli radiating from the annuli. Septa often double, with an interspace between the two layers near the siphuncle, but solid near the shell. Ordovician to Carboniferous.

Fig. 1078.

Actinoceras vertebratum, Hall. Silurian; Lockport, New York. Longitudinal section showing organic deposits of siphuncle (after Barrande).

Sub-genera: *Ormoceras*, Stokes (Fig. 1079). Ordovician to Carboniferous. *Paractinoceras*, sub-gen. nov. (Fig. 1080). Shells longer and more slender

Fig. 1079.

Actinoceras (*Ormoceras*) *Bayfieldi*, Stokes. Ordovician; Lake Huron, Canada. Longitudinal section showing organic deposits of siphuncle partly dissolved away (after Stokes).

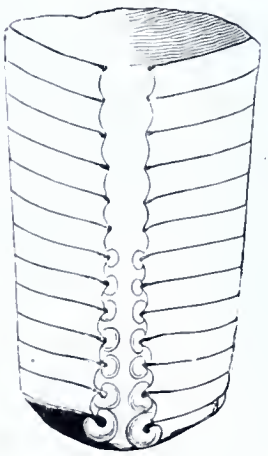


Fig. 1080.

Actinoceras (*Paractinoceras*) *docens*, Barr. sp. Silurian (E); Dvoretz, Bohemia. Vertical section showing senile stage without organic deposits, preceded by adult stage with siphuncular rosettes (after Barrande).

Fig. 1081.

Huronia vertebralis, Stokes. Ordovician; Isle Drummond, Lake Huron. Siphuncle.

than in the preceding, with large siphuncular segments confined to early stages, and very long living chamber. Type *P. (Sact.) canadense*, Whiteaves sp. Silurian.

Cyrtactinoceras, gen. nov. Type *C. (Cyrt.) rebelle*, Barr. sp. *Deiroceras*, Hyatt; *Huronia*, Stokes (Fig. 1081); *Discosorus*, *Gonioceras*, Hall. Silurian.

(?) *Tretoceras*, Salter. Orthoceracones having a centren nummuloidal siphuncle, similar to that of *Aetinoceras* but smaller, and with a superficial tubular siphuncle (so-called), having very long but not Holochoanoidal funnels. Sheath not yet shown to be present. It is possible that the structure referred to is a peripheral pseudo-siphuncle formed by abnormal condition of the septa. Silurian.

II. Actinosiphonata.

Orthoceracones, cyrtoceracones, gyroceracones, and a few discoidal nautilicones. Shells frequently breviconic, in which case gerontic living chambers and apertures are more highly contracted than in all other Nautiloids. Siphuncle sometimes empty; organic deposits when present in the form of laminae radiating from the sheath of each segment towards the interior. These internal calcareous septa are united only in their peripheral parts, not meeting at the central axis so far as known, and also liable to be more or less interrupted in the transverse plane of each funnel. The interior is consequently an actiniform endosiphuncle with rays extending outwardly between the laminae of the deposits.

Family 4. **Jovellanidae.**

Orthoceracones and cyrtoceracones with slightly compressed oval, or depressed and more or less sub-trigonal sections. Shells smooth or partially annulated. Siphuncle large, with well-developed actiniform lamellae, and distinct endosiphuncles. Aperture open and living chamber uncontracted in gerontic stage.

Includes *Jovellania*, Bayle; *Tripleurocroceras*, Hyatt. Silurian and Devonian. *Mixosiphonoceras*, gen. nov. Type *M.* (*Cyrt.*) *desolatum*, Barr. Silurian and Devonian. *Projovellania*, gen. nov. Type *P.* (*Cyrt.*) *athleta*, Barr. Silurian.

Family 5. **Rizoceratidae.**

Orthoceracones and cyrtoceracones expanding regularly by growth throughout life, the living chamber very slightly or not sensibly contracted in gerontic stage. Aperture constantly open, and with slight dorsal as well as somewhat deeper and broader hyponomic sinuses. Siphuncle generally small and empty, but actiniform lamellae and an endosiphuncle sometimes occur. Shells as a rule smooth or with transverse bands only, but longitudinal striae often present in earlier stages.

Rizoceras, Hyatt (Fig. 1082). Orthoceracones and exo- or endogastric cyrtoceracones having circular or elliptical sections. Living chamber extraordinarily large and long as compared with camerated part. Silurian to Carboniferous.

Cyrtorizoceras, gen. nov. Sections more compressed than in *Rizoceras*, living chamber shorter and apt to be more or less laterally compressed in gerontic stage, but the dorso-ventral diameters only very slightly so or not at all. Sutures more sinuous, and with decided ventral and dorsal saddles. Type *C.* (*Cyrt.*) *minneapolis*, Clarke sp. Ordovician and Silurian.

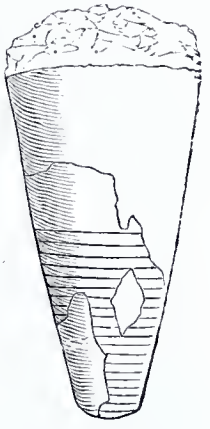


Fig. 1082.

Rizoceras robustum. Barr. sp. Silurian (E); Butowitz, Bohemia. Aperture open. 1/2.

Family 6. **Ooceratidae.**

Orthoceracones and gyroceracones with closely set septa and large nummuloidal siphuncle in later stages of the ontogeny, but tubular in the young. Actiniform deposits oftener present than in Rizoceratidae, but not general. Funnels very variable, sometimes minutely plicated or hook-like in section, confined to dorsal side of

tube, or sometimes absent altogether. Living chamber short and like that of Cyrtorizoceras; aperture not infrequently sub-trigonal in outline, but always open.

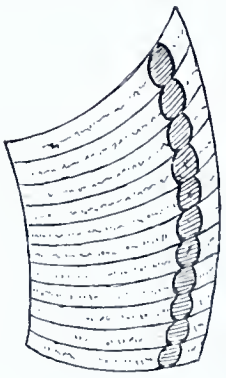


Fig. 1083.

Ooceras (Cyrt.) Baylei, Barr. sp. Silurian (E); Lochkow, Bohemia (after Barrande).

Ooceras, Hyatt (*Oonoceras*, Hyatt), (Fig. 1083). Cyrtoceracones more elongated and usually more compressed than in *Cyrtorizoceras*, but otherwise similar except in structure of siphuncle. Septa rise rapidly on ventral side, and may bend sharply orad, forming a funnel ridge or shoulder on that side, but disappearing on the opposite side of the same funnel. When the funnel itself is absent, the ridges look like reversed funnels or collars. Silurian.

Cyrtoceras, Goldf. Large exogastric, breviconic cyrtoceracones; sections depressed elliptical or approximating to trigonal, the dorsum more or less flat, and venter elevated. Aperture contracted in gerontic stage to a T-shaped opening, and placed at an acute angle with the central axis, so that the dorsal side is very much shorter than the ventral. Siphuncle large, nummuloidal, with well-developed actiniform lamellae, and with an endosiphuncle in later stages of ontogeny. Devonian.

Family 7. Oncoceratidae.

A phylogerontic group of breviconic orthoceracones and cyrtoceraeones similar to Cyrtorizoceras, but shells much shorter and living chamber usually contracted, especially in their transverse diameters during gerontic stage. Siphuncle tubular or highly nummuloidal, without deposits.

Eremoceras, gen. nov. Cyrtoceracones similar to *Cyrtorizoceras*, but living chambers longer, and aperture more or less flaring and open. Siphuncle more or less nummuloidal. Type *E. (Cyrt.) syphax*, Bill. sp. Ordovician.

Cyclostomiceras, gen. nov. Slender, short, exogastric orthoceracones and cyrtoceracones, circular or compressed in section. Living chamber as compared with camerated part longer and larger than in most forms, less contracted, and with open aperture in gerontic stage. Type *C. (Pot.) cassinense*, Whitf. sp. Ordovician to Devonian.

Oncoceras, Hall. Compressed exogastric cyrtoceracones with sections like *Cyrtorizoceras*, but shells as a rule much shorter and smaller, and siphuncle more distinctly nummuloidal. Living chamber also more flattened laterally, the aperture elongated and often sub-trigonal, but typically open. Ordovician.

Sub-genus: *Meloceras* (*Melonoceras*), Hyatt. Similar to the last, but lateral edges of gerontic aperture grow inwards, and form pear-shaped outlines. Silurian.

Family 8. Poterioceratidae.

Smooth, breviconic orthoceracones and cyrtoceracones having circular or depressed elliptical sections. Gerontic aperture, except in primitive forms, is contracted and apt to assume a sub-trigonal outline; it is laterally narrowed and approximates those of the next family only in Streptoceras. Outlines of aperture entire; sutures straight or only slightly sinuous. Siphuncle in this and remaining families, so far as known, slightly nummuloidal and empty in the young, but becomes larger; in specialised forms it is apt to be more or less filled with radiating lamellae, and in late stages has an endosiphuncle.

Clinoceras, Mascke. Ordovician to Devonian. *Sycoceras*, Pictet. Devonian.

Poterioceras, M'Coy (*Apioceras*, Fischer; *Acleistoceras*, Hyatt). Orthoceracones and exogastric cyrtoceracones, short and stout, with sub-trigonal gerontic aperture. Brachial area not decidedly differentiated from the hyponomic sinus, and contraction may take place in all diameters or more extensively in the lateral. Ordovician to Carboniferous.

Streptoceras, Bill. Like the last but more arcuate, with laterally contracted aperture, and a short hyponomic sinus distinct from the brachial area. Silurian.

Family 9. Trimeroceratidae.

Smooth breviconic orthoceracones and cyrtoceracones similar to Poterioceras in aspect and sutures, but more slender, especially in the young, and aperture very distinct in primitive forms. Even the latter usually have brachial distinctly marked off from hyponomic area by ingrowth of sides of the aperture, and in all specialised shells the hyponomic sinus and special inflections known as "brachial sinuses" are formed by bases of the arms on edges of brachial area. Finally, the aperture becomes reduced to a more or less Y- or T-shaped figure, with an open semicircular sinus at the end of the hyponomic slit or area, and similar sinuses in the edges of the brachial slit, corresponding to the number of arms. All Silurian.

Mandaloceras, Hyatt (*Dimorion*, Barr.), (Fig. 1084). Differs from *Poterioceras* in the gerontic aperture, which is laterally contracted, and has hyponomic and brachial areas distinctly differentiated in all but the most primitive species. More specialised forms have these areas narrowed down, but special sinuses are not formed.

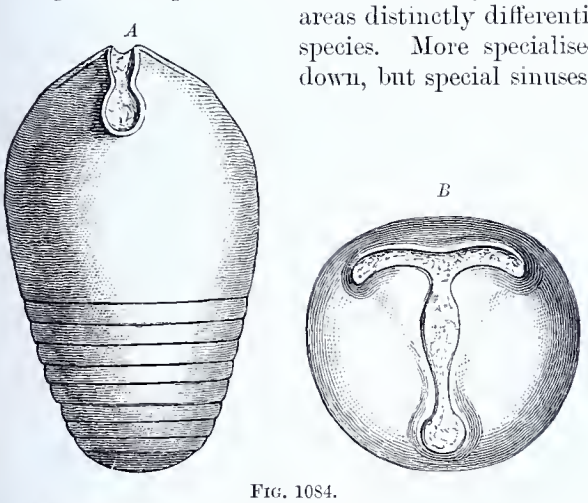


Fig. 1084.

Mandaloceras (*Gomph.*) *Bohemicum*, Barr. sp. Silurian (Étage E); Dvoretz, Bohemia. *A*, Side view of conch. *B*, Aperture.

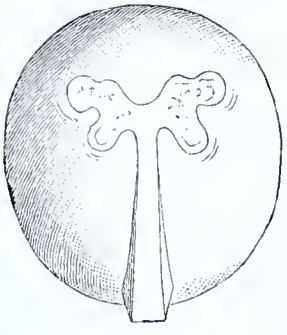


Fig. 1085.

Tetrameroceras Panderi, Barr. sp. Silurian (E); Dvoretz, Bohemia. 1/1 (after Barrande).

Trimeroceras, Hyatt (*Trimorion*, *Trimeres*, Barr.); *Pentameroceras*; *Septameroceras*, Hyatt. Silurian. Aperture in the first has a median and two brachial; in the second a median and four brachial; and in the last a median and six brachial sinuses.

Hemiphragmoceras, gen. nov. Compressed endogastric cyrtoceracones having a narrowed hyponomic area like *Phragmoceras*, but with brachial areas as in *Dimeroceras*. Type *H.* (*Phrag.*) *pusillum*, Barr. sp.

Tetrameroceras, Hyatt (*Tetramorion*, *Tetrameres*, Barr.), (Fig. 1085). Like the last, but with more highly contracted aperture and four lateral sinuses.

Hexameroceras, Hyatt. Brachial area with six lateral sinuses. *Octameroceras*, gen. nov. Brachial area with eight lateral sinuses. Type *O.* (*Phragm.*) *callistoma*, Barr. sp.

Family 10. Phragmoceratidae.

Smooth breviconic cyrtoceracones and gyroceracones rapidly expanding by growth in their dorso-ventral diameters, and having open apertures only in primitive types or the young and ephebic stages of more specialised forms. In the latter gerontic apertures are laterally contracted and have a very long hyponomic area terminated by a large hyponomic sinus. The brachial area may be more or less open and elliptical, or

narrowed and transversely elongated, but always has an entire outline. Siphuncle generally large, nummuloidal, and often has actiniform lamellae and endosiphuncles in later stages. Shells mostly endogastric.

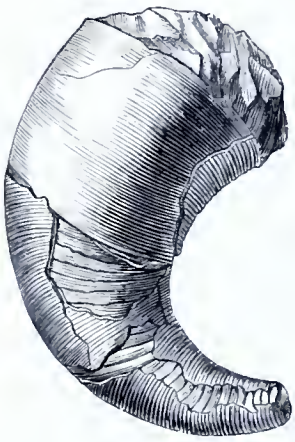


Fig. 1086.

Protophragmoceras Murchisoni, Barr. sp. Silurian (E); Lochkow, Bohemia. 1/2.

Codoceras, gen. nov. Excessively short and rapidly expanding cyrtoceracones like some species of *Rizoceras*, but with large living chambers, narrow venter, and large siphuncle just ventrad of centre. Aperture constantly open. Type *C.* (*Cyrt.*) *indomitum*, Barr. sp. Silurian.

Protophragmoceras, gen. nov. (Fig. 1086). Similar to the last, but form more compressed, and siphuncle near the venter (internal). Differs from *Phragmoceras* in having aperture open throughout life. Type *P.* (*Cyrt.*) *Murchisoni*, Barr. sp. Silurian.

Gomphoceras, Sowb. Stout short orthoceracones and cyrtoceracones similar to some species of *Phragmoceras*, but straighter, stouter, and less compressed in form, and gerontic aperture less contracted laterally. Hyponomic sinus shorter, and curvature exogastric. Ordovician and Silurian.

Phragmoceras, Sowb. (Figs. 1087, 1088). Compressed endogastric cyrtoceracones and gyroceracones, oval in section, and venter narrowly

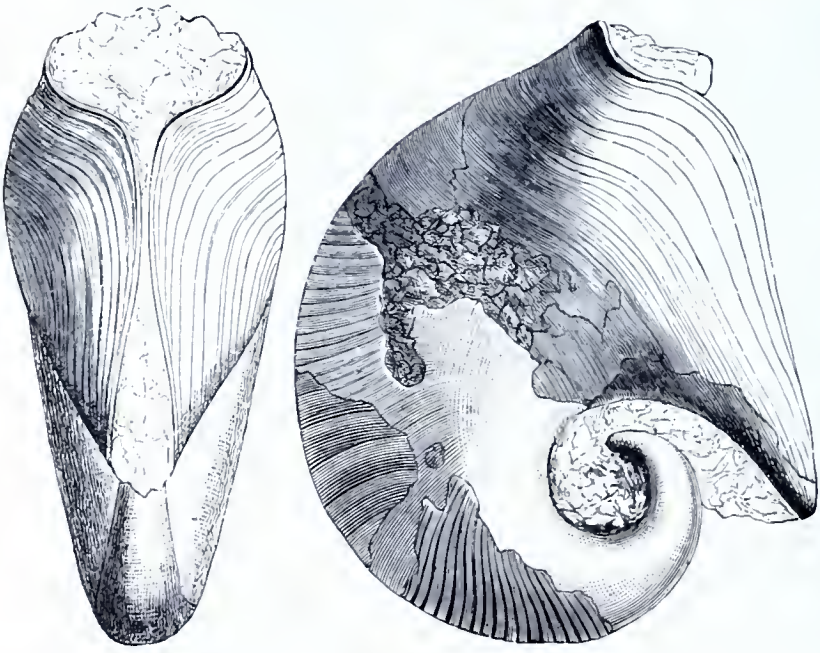


Fig. 1087.

Phragmoceras Brodcripi, Barr. Silurian (Étage E); Lockhow, Bohemia. 1/2 (after Barrande).

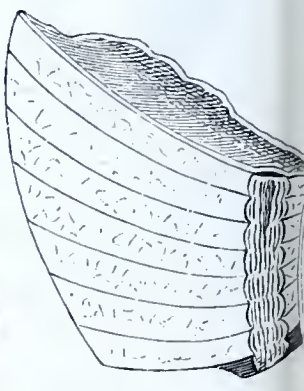


Fig. 1088.

Phragmoceras Loveni, Barr. Silurian (E); Lochkow, Bohemia. Section showing lamellar organic deposits (after Barrande).

rounded. Siphuncle large and near the venter (internal). Gerontic aperture much contracted laterally, the hyponomic area very long and narrow. Silurian.

Incertae Sedis.

Nothoceras, Barr. Represented by the single species *N. bohemicum*, Barrande, in which the septum turns orad, forming an inverted funnel. This funnel connects with

a more or less inflated sheath that closed the siphuncle, and connected it with the distal opening of the next succeeding septum, thus completely reversing the relative positions of funnels and sheaths in other forms. The appearances as described by Barrande are not deemed sufficient to prove the truth of this statement, and it is unsafe to accept it absolutely until the development has been studied. The cavity is divided by radiating lamellae running longitudinally as in the *Actinosiphonata*.

Range and Distribution of the Nautiloidea.

Fossil *Nautiloidea* have been recorded by Billings as occurring in Canada earlier than the Quebec Group, but his statement lacks confirmation. An abundant Cephalopodan fauna makes its appearance in the earliest Quebec or Calciferous, and is quite distinct from other later assemblages. *Diphragmoceras* and other orthoceracones and cyrtoceracones with very peculiar siphuncles occur here, but gyroceracones and nautilicones are absent. However, the information we have at present of this fauna is limited, and but few positive conclusions can be drawn.

All the sub-orders of *Nautiloidea* are initiated in the Ordovician, and one of them, *Schistochoanites*, is confined to this period. *Holochoanites* and *Mixochoanites* become extinct in the Silurian, and only *Orthochoanites* survive the Palaeozoic. The sub-orders that disappear at this early date are remarkable for their complicated siphuncular structure, and peculiar sigmoidal septa observed in the gerontic living chambers of certain forms (*Ascoceras*, *Gonioceras*), while their prevailing habit is gyroceraconic. The sigmoidal septa do not become complicated in correlation with closer coiling of the shell, but occur in cyrtoceracones correlating with highly compressed cones, and in orthoceracones correlating with strongly depressed cones.

The older classifications recognised the straight orthoceracones, curved cyrtoceracones, loosely coiled gyroceracones, and more closely coiled nautilicones as distinct natural divisions. Although it is possible to employ the habit of curvature in conjunction with family groups as a convenient means for tracing laws of distribution and the like, yet for more accurate data the genera must be considered independently. For instance, some families made up largely of gyroceracones and nautilicones also contain a few orthoceracones and cyrtoceracones, and these have to be neglected in estimating the relative proportions of straight and coiled conchs. Other sources of error are presented by sporadic uncoiled or gerontic forms which occur in families having coiled shells. In a general way, however, it is possible to state the morphic succession as follows :—

Orthoceracones, together with their almost invariably associated cyrtoceracones exceed gyroceracones in the Quebec in the proportion of three families to one, and this horizon contains but one family of closely coiled nautilicones, and one of the uncoiled or gerontic type. In the Ordovician are found no less than fourteen families having straight or approximately straight shells, as against seven families of gyroceracones and nautilicones. Thereafter until toward the close of the Palaeozoic, the proportions of straight and coiled forms remain approximately equal. The Permian has but one surviving family of orthoceracones, and four of the coiled groups ; in the Trias the ratio is one to six, and in the Jura coiled forms alone persist. Thus, a slowly working tendency is apparent, leading to the production of more and more closely coiled cones, and the elimination of straight and slightly curved forms. Gyroceracones disappear with the Carboniferous, and the more discoidal nautilicones with the Trias.

Some curious features are presented by the phylogerontic or uncoiled shells. Only one family, the Silurian *Lituitidae*, have all the genera uncoiled save the probable ancestral close-coiled type. Other families have isolated genera or species exhibiting similar tendencies, and becoming partially uncoiled during their later stages, although close-coiled in the young. Such forms occur throughout the Devonian, but none have

yet been found in the Carboniferous, where uncoiling of the volutions, when it occurred, took place earlier than the gerontic stage. From the Mesozoic and later horizons, no species is known in which the gerontic stage is to the slightest degree uncoiled.

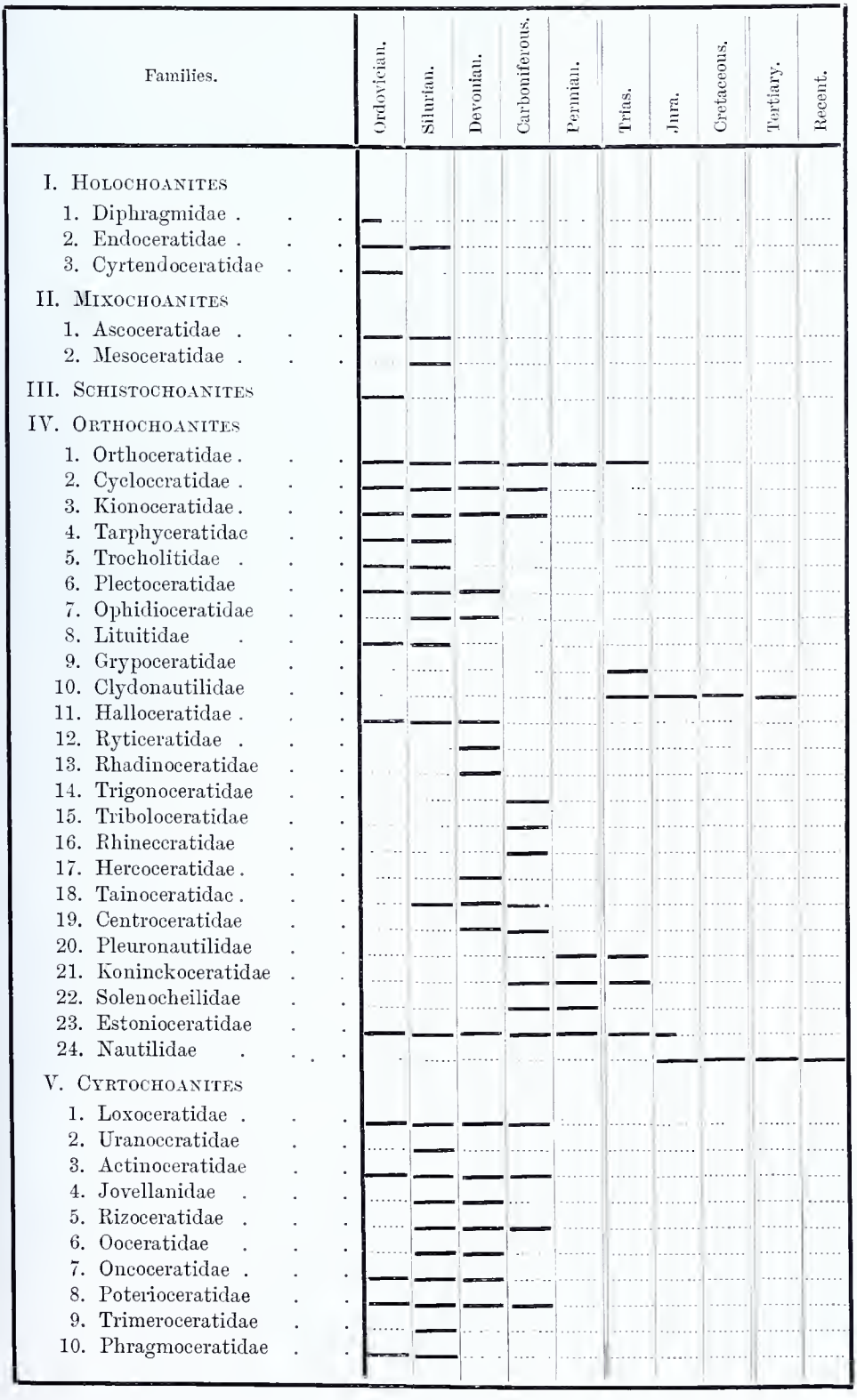
Torticones are more aberrant than any other conchs, and may be best classified as phylogerontic forms, since tendencies toward unsymmetrical development of the volutions occur in the gerontic stage, and are genetic in but a few genera, where they appear during the early stages and are preceded so far as known by a symmetrical volution. The first manifestation of torticones is in the Ordovician, and their acme is attained during the Silurian. As regards ornamentation, annulated shells appear in the Calciferous, and those with longitudinal ridges later in the Ordovician, together with tuberculated and costated gyroceracones and nautilicones. The last-named, however, are much more abundant in the Devonian and Carboniferous, after which they disappear. Very highly ornamented shells exist in the Trias, but following this period the conchs are smooth.

Very striking is the marvellously sudden rise of the *Nautiloidea* as a group, reaching its maximum in the Silurian, and followed by a decline extending from the Devonian to the Trias. Then the forces acting unfavourably upon their existence were arrested, or their violence lessened, and the group has been affected by only very slight changes and an exceedingly slow process of retrogression until the present time. The acme of siphuncular differentiation occurred in the Ordovician, of general morphic diversity in the Silurian, of ornamentation in the Devonian, and of sutures in the Trias.

Geographically considered, some facts of distribution are of general interest. The fauna of the Quebec or Calciferous, which in Newfoundland, Canada, Vermont, and the vicinity of Poughkeepsie, New York, is rich in fossil remains, is represented by but a few camerated conchs in the Durness Limestone of Scotland. *Holochoanites* and *Schistochoanites* are most plentifully represented in the American faunas, but *Mixochoanites* very sparsely so, at least as compared with the Ordovician and Silurian of Bohemia. The same is true of the *Lituitidae*, *Ophidioceratidae*, and *Hercoceratidae* among *Orthochoanites*, and of the *Jovellanidae*, *Trimeroceratidae*, and kindred families among the *Cyrtochoanites*. The Devonian and Carboniferous faunas of America and Europe are nearly on a par, but the Permian and Trias of the western hemisphere are very deficient in Nautiloid remains. The Jurassic faunas of America have so far yielded but one specimen of a Nautiloid, but they were probably present to some extent, since they are represented in the Cretaceous of this country. During the Cretaceous and Tertiary the principal distribution of the *Nautilidae* was in the eastern hemisphere, and the last surviving species of *Nautilus* are now restricted to oriental waters. The accompanying table shows the range of the leading Nautiloid families.

[The *Hercoceratidae* occur in the Devonian, and not in the Silurian rocks, as is stated through an oversight on page 524.]

TABLE SHOWING VERTICAL RANGE OF THE NAUTILOIDEA.



Order 2. AMMONOIDEA.[1]

Shells similar to those of Nautiloidea in some primitive Palaeozoic groups, but these give rise to others with more highly ornamented shells, the apertures of which have ventral rostra instead of hyponomic sinuses. Sutures, as a rule, have ventral lobes in the later stages of ontogeny; the inflections become more numerous than in Nautiloids even in Palaeozoic genera, and their outlines during the Mesozoic are extremely complex. Siphuncle invariably small, and (except in Gastrocampyli) situated near the venter. Funnels short, monochoanitic in primitive forms, but becoming diplochoanitic during the Palaeozoic, and as a rule, chloiochoanitic during the Mesozoic.

The ontogeny begins with a calcareous protoconch, the apical stage of the conch being an open neck built in continuation of the permanent aperture of the protoconch. The first septum is concave as in Nautiloids, and sutures are straight or have more or less of a saddle on the venter. Young stages of Mesozoic shells recapitulate the primitive characters of Palaeozoic forms. The aperture was closed when the animal was retracted by a single horny plate (*anaptychus*) or pair of calcareous plates (*aptychus*), probably secreted by muscular lobes homologous with the hood in *Nautilus*.

Shell Characters.—There are apparently no characters, not even the presence of a calcareous protoconch, which can be relied upon to separate *Bactrites* from the orthoceraconic Nautiloids. Nevertheless, the position of the siphuncle and its peculiar funnels are features which seem to place this form with true Palaeozoic Ammonoids. There is but one series of straight shells among Ammonoids, and these are obviously not the same as orthoceracones, but are more properly called *bactriticones* (Fig. 1120). Similarly, the loosely coiled *Mimoceras* shells (Fig. 1121) are not gyroceracones, but only their morphic equivalents in a different genetic stock; hence the term *mimoceracone* should be substituted for gyroceracone. In the same sense the closely coiled symmetrical shells, comparable in external aspect and intimate structure with nautilicones, should be described among Ammonoids as *ammoniticones*. The term *torticone*, however, can be conveniently applied to both groups, since it does not connote any special structures, but is a general name for all asymmetrical spirals.

Ammoniticones in many Palaeozoic forms are mimoceracones during nepionic stages, and consequently in later stages a perforation is present passing through the umbilicus as in Nautiloids. However, in most Carboniferous and all later ammoniticones, the coiling is so close even at the beginning of the conch, that the protoconch is closely enwrapped by the first volution,

[1] Besides the works cited on pp. 502-505, the following may be profitably consulted:—*Buckman, S. S.*, Divisions of so-called Jurassic Time (Quar. Journ. Geol. Soc., LIV.), 1898.—*Clarke, J. M.*, The Naples Fauna (16th Ann. Rep. N.Y. State Geologist), 1898.—*Crick, G. C.*, Muscular Attachment of the Animal to its Shell in Ammonoidea (Trans. Linn. Soc. [2], VII.), 1898.—*Diener, C.*, Cephalopoda of the Muschelkalk (Mem. Geol. Survey India, ser. XV., Himalaya Fossils, II.), 1895.—*Haug, E.*, Études sur les Goniatites (Mém. Soc. Géol. France, Paleont., VII.), 1898.—*Levi, G.*, Fossili degli strati a Terebratula aspasia (Boll. Soc. Geol. Italia, XV.), 1895.—*Parona, C. F.*, and *Bonarelli, G.*, Faune du Callovien inférieur (Chanazien) de Savoie (Mém. Acad. Savoie, VI.), 1897.—*Semenoff, B.*, Anwendung der statistischen Methode zum Studium der Vertheilung der Ammoniten (Ann. Geol. Mineral. Russie, II.), 1897.—*Smith, J. P.*, Development of Lytoceras and Phylloceras (Proc. Calif. Acad. Sci. [3], I.), 1898.—*Choffat, P.*, Les Ammonées du Bellasien, des Couches à Neolobites Vibrayeanus, du Turonien et du Sénonien. Faune crét. du Portugal, vol. I. ser. II., 1898.—*Jackson, R. T.*, Localised Stages of Development in Plants and Animals (Mem. Boston Soc. Nat. Hist. V.), 1899.

and no perforation is visible even under a magnifier. There are two pits, however, one on either side of the apical end of the conch, which remain as remnants of this perforation, and are present in all ammoniticones (except perhaps certain *Gastrocampyli*). The bactriticone obviously represents the primitive or primary radical of the *Ammonoidea*, and the mimoceracone the next or secondary radical of this order.

Ammoniticones of the *Microcampyli* introduce a peculiar form of volution, the *anarcestean* (Fig. 1122), which is depressed and crescentic in section, and may be regarded as the Tertiary radical. These forms evolve a series becoming more involute and compressed (Fig. 1123), and some with elevated or narrow venters and well-defined lateral zones (Fig. 1124), but still retaining in the young more or less of the anarcestean aspect. The *Gastrocampyli* have a few radical forms of similar aspect and with somewhat similar sutures (Fig. 1116); they then produce a series of compressed discoidal shells having cordiform or quadrate sections (Figs. 1117-1119), and these also develop involute forms among specialised species. The *Mesocampyli* and *Glossocampyli* have a similar history, but in the *Eurycampyli* coronate or gastrioceran forms (representing a quaternary radical) with trapezoidal section and broad venter become common in the ephebic stages (Fig. 1132). The primitive radical forms of the anarcestean ammoniticones are replaced among the *Phyllocampyli* by the smooth, discoidal, compressed quinary radical, or *prolecanitean* type (Fig. 1155). This appears among the adult *Gastrocampyli*, although with distinct sutures, and is also found among the *Discocampyli*. In the more specialised sub-orders, the anarcestean type reappears only during the young stages. These last two

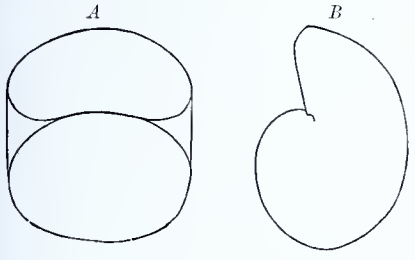


FIG. 1089.

Asellate protoconch of *Gephyroceras calculiforme*, Beyr. sp. Upper Devonian; Büdesheim, Eifel. *A*, Viewed from in front. *B*, From the side (after Branco).

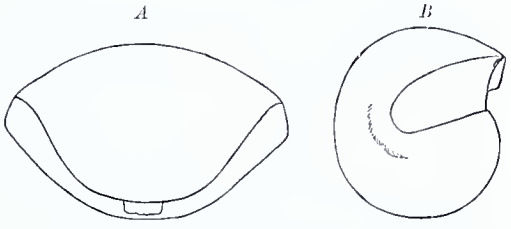


FIG. 1090.

Latisellate stage of *Arcestes cymbiformis*, Wulfen sp. Trias; Aussee, Austria. *A*, Viewed from in front. *B*, From the side (after Branco).

radicals persist into the Jura and Cretaceous, but exhibit more complex sutures and other progressive structural changes in their ephebic stages.

Phylogerontic series (*Rhabdoceras*, *Cochloceras*) make their appearance in the Upper Trias, become more abundant in the Jura, and still more important during the Cretaceous. They have their own peculiar radicals, sometimes found among discoidal and again among more involute shells, but for the most part they do not originate from smooth shells.

The same descriptive terms are used for shell characters among Ammonoids as among Nautiloids (see p. 512 *et seq.*). Obviously the first stage of the conch was that of a living chamber, the protoconch being without internal septa or siphuncle (Fig. 1101). Then, after building out the usually flattened neck or apical part of the conch, the animal rested, and the first septum as well as the *caecum* (or incipient stage of the siphuncle) was secreted. The first

septum closed the aperture of the protoconch, and the caecum projected into its interior. The caecum is connected with the internal surface of the protoconch by bands (Figs. 1101, 1102), or semiconical prolongations, described by Munier-Chalmas as the *prosiphon*. But these bands are of various shapes, are not connected with the interior of the caecum, and appear to be merely calcareous supports for the bottom of the caecum. The earliest sutures, described in a masterly way by Branco, are divided by him into three classes: *asellate*, *latisellate*, and *angustisellate* (Figs. 1089-1091). The first cross the venter as a straight line or very slight saddle, and are present only in the ephebic stages of *Cyrtoclymenia* (?) and in the mimoceran stage of the *Microcampyli*. In all except primitive forms it is confined (as are most of the purely nautiloidean characters) to the first septum. The latisellate stage is characterised by a decided broad saddle on the venter, with corresponding deeper and broader lobes on the sides. The angustisellate stage has prominent, sometimes almost sub-acute ventral saddles with corresponding deep lateral lobes, accompanied by definite saddles at the umbilical depressions.

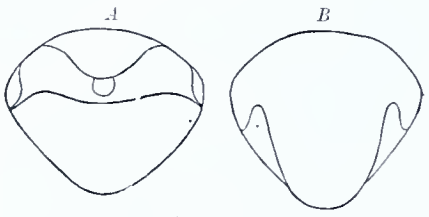


Fig. 1091.

Angustisellate stage of *Phylloceras heterophyllum*, Sow. sp. Lias.

The last two stages are progressive modifications confined to the larvae of Ammonoids, and are not present in the ephebic stages of any known species. The asellate condition of the first septum is found in the ananepionic stage of one species of the *Gastrocampyli*, according to Branco, but his figure shows a saddle on the venter. The *Microcampyli* and *Mesocampyli* are asellate, and the *Eurycampyli* also in some primitive Devonian genera, but latisellate in others, and angustisellate in the Trias. The embryos of primitive *Phyllocampyli* are unknown, but the Triassic *Lobitidae* and *Arcestidae* are latisellate, while the *Cladiscitidae* and the *Phylloceratidae* are angustisellate throughout. The embryos of *Discocampyli* are almost unknown, but are supposed to be latisellate, with the exception of the highly specialised *Pinacoceratidae*, which are angustisellate. The remaining sub-orders are wholly Jurassic and Cretaceous, and so far as known, the first septa are angustisellate.

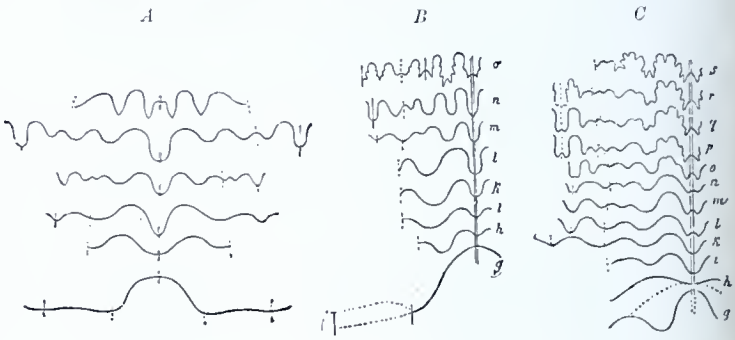


Fig. 1092.

A, Development of sutures in a latisellate Goniatite (*Glyphioceras diadema*, Goldf. sp.). Carboniferous Limestone; Choquier, Belgium. *B*, Same in a latisellate Ammonite (*Tropites subbullatus*, Hauer). *C*, Same in an angustisellate Ammonite (all after Branco). Sutures of the first volution are lettered consecutively from *g* to *l*; those of the second from *m* to *s*.

Sutures.[1]—The second septum (Fig. 1092) in all but the most primitive

[1] [The nomenclature commonly in vogue designates the sutural inflections as follows:—The *ventral* or *external* lobe is bounded on either side of the mesal plane by the large *first* or *superior-lateral* saddle. This is followed by the first or superior-lateral lobe, and then come the *second* or *inferior-lateral* saddle and lobe in the order named. All additional inflections occurring between the second

forms becomes divided by an entire azygous lobe on the venter, often termed the "siphonal lobe," but herein after referred to as the *ventral lobe*, and by a smaller azygous lobe (shown to the left in Fig. 1092, *A-C*) on the dorsum, usually termed the *antisiphonal*. This undivided ventral lobe (Figs. 1094, 1095, *EL*) persists throughout the *Microcampyli* so far as known, and is obliterated by a secondary ventral saddle only in the *Gastrocampyli*. It is present throughout the ontogeny of the simplest or radical forms of *Eurycampyli*, *Glossocampyli*, and *Phyllocampyli*. But in the Devonian *Mesocampyli* and Triassic *Discocampyli*, shells having undivided ventral lobes have not been recorded; in the *Tirolitidae* but one such species has been doubtfully described. This class of radicals is replaced in these sub-orders by those having the ventral lobe divided by a small saddle usually called the ventral or *siphonal saddle* (Fig. 1097, *m*). The class of radicals having entire ventral lobes disappears before the close of the Trias.

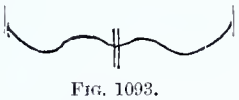


Fig. 1093.

Suture-line of *Cyrtoclymenia laevigata*, Münst. Devonian.

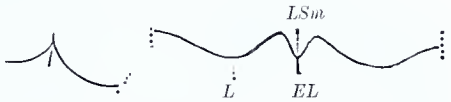


Fig. 1094.

Suture-line of *Anarcestes subnautilinus*, Schloth. sp. Devonian.

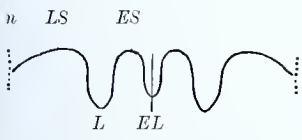


Fig. 1095.

Suture-line of *Brancoceras sulcatus*, Münst. sp. Devonian.

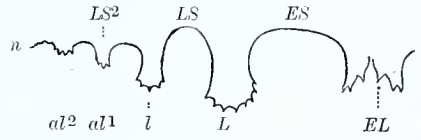


Fig. 1096.

Left half of suture-line of *Ceratites nodosus*, de Haan. Trias.

The entire antisiphonal lobe has a more extensive distribution than the entire ventral lobe, being present throughout the ontogeny of *Microcampyli*, *Gastrocampyli*, and *Mesocampyli*. Most of the *Eurycampyli* have this lobe entire, but it becomes bifid in the later stages of specialised forms. The radicals of *Glossocampyli* have it entire, but in specialised genera it becomes bifid or even trifid. It is known to be entire in only a few of the *Lecanitidae*, and is bifid in most of the *Discocampyli* and *Phyllocampyli*, besides having for the most part entire sides. It is also entire in some phylogerontic species of the Trias. In the *Leptocampyli* it is generally bifid, but may be trifid or irregular in some species, and is accompanied by an extraordinary growth of two of the branches inwards in a large number of forms. In Jurassic and Cretaceous Ammonoids, it is as a rule more or less

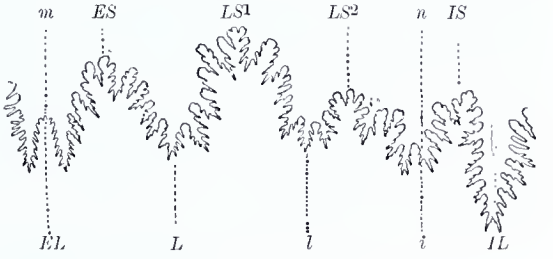


Fig. 1097.

Right suture-line of *Coroniceras bisulcatum*, Brug. Lias. *m*, Siphonal saddle; *n*, Line of involution. *EL*, Ventral (also called siphonal or external) lobe, traversed by the siphuncle. *L*, First or superior-lateral lobe; *l*, Second or inferior-lateral lobe. *ES*, LS^1, LS^2, First, second, and third lateral saddles. *IS*, Dorsal saddle. *IL*, Antisiphonal lobe. *i*, First dorsal lobe lying on line of involution.

lateral lobe and the line of involution are termed *auxiliaries*, and numbered in regular order. The antisiphonal is also known as the *internal*, *dorsal*, or *columellar* lobe. By "lobes" are always understood the angulated or digitated portions of the suture which are directed *backwards*, away from the mouth of the shell; "saddles" are the elevations between them, which point *towards* the aperture of the shell.—Trans.]

complicated by the development of secondary inflections on the sides, termed *marginals*.

Paired or zygous lobes and saddles (Fig. 1092) appear between the two azygous lobes and belong to two series, the *laterals* or externals, and the *dorsals*. The first broad external lateral inflections, called the "first pair of lateral saddles," are formed by the ventral lobe and the corresponding first pair of dorsals by the formation of the antisiphonal lobe; and between these there appears a broad lobe, either wholly or the most part external (Fig. 1092, *A*). This is the stage marked by four lobes and saddles—two azygous and two zygous lobes, and four zygous saddles. The wide lateral lobes in the next stage (Fig. 1092, *Ck*) are divided by saddles that arise on or near the lines of involution. These divide the two lobes into four, one pair being in part or wholly dorsal, and becoming eventually the first pair of dorsal lobes; the others develop into the "first pair of lateral lobes." There are accordingly six lobes and six saddles at this stage. In the next stage (Fig. 1092, *A*, *Bm*, *Cm*) the saddles bridging the lines of involution become divided by lobes arising on or near the lines of involution, and the inner arms of the saddle so formed thus become the second dorsal saddle, while the outer form the *second lateral saddles;* but in some forms they may both pass into the lateral series. This stage, therefore, has eight lobes and eight saddles—three paired lobes and four saddles on either side of the mesal plane, and two azygous lobes.

Additional inflections arise in like manner along or near the line of involution during succeeding stages. But there is considerable irregularity in their advent even in the eight-lobed stage, and still more so at later periods; hence the above description must be regarded as a very general one, although serving to indicate a few primitive lobes and saddles that are generated during the younger stages, and are usually recognisable in the adult.

In subsequent stages additional inflections arising on or near the lines of involution pass outward as the sides of the shell broaden by growth; and the

Fig. 1098.

Pinacoceras Metternichi, Hauer sp. Keuper; Someraukogel, near Hallstadt, Austria. Left suture-line, much reduced, showing auxiliary (inner) and adventitious (outer) inflections. The three longest lobes in the middle are the first, second, and third laterals (after Hauer).

same law holds true for the dorsum, but of course here the inflections pass inward toward the mesal plane. The number of inflections on the dorsum is more limited in all forms than the laterals, and they have simpler outlines. The inflections added to the sides after the first two or three saddles and lobes appear are usually called the *auxiliaries* (Figs. 1096, *al*, 1098), but the current use of this term is not consistent with the development of the inflections, and the distinctions are based for the most part on the contrast in size between the saddles and lobes as they appear in the adult of different types. When the ontogeny is known, however, the auxiliary inflections can be properly

discriminated and described, but otherwise are liable to confuse the nomenclature. Adventitious inflections (Fig. 1098) arise between the first pair of laterals and the median line of the venter, either by the growth of marginals in the arms of the ventral lobe, or by division of the outer parts of the first lateral saddles, or by division of the inner parts of the siphonal saddle.

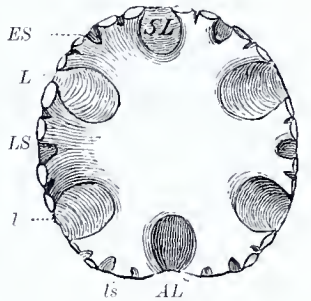


Fig. 1099.

Lytoceras fimbriatum, Sowb. sp. Middle Lias; Wurtemberg. Transverse section of volution. *SL*, Ventral lobe; *AL*, Antisiphonal lobe; *L*, Superior lateral lobe; *l*, Inferior lateral lobe; *ES*, External saddle; *LS*, *ls*, First and second lateral saddles.

The regions of greatest metabolism or growth-changes in each genetic series are near the lines of involution, and it is here that new inflections are usually formed. The later formed lobes and saddles in these regions repeat in their own development the ontogenetic stages of modification through which the older ones have already passed. It follows also from this that the lobes and saddles nearest the umbilical lines of involution are simple and often entire, and are parts of a series that become progressively more complicated outwards to the lines or columns of the oldest class—the first lateral lobes and saddles. When there are adventitious lobes, this series is reversed on the ventral side of the first pair of saddles. The inversion is sometimes quite complete, as in some of the *Glossocampyli*, thus indicating unusual metabolism on the venter like that of the regions of involution. Jackson's law of the localised recapitulation of ontogenetic stages is well exemplified by the history of sutures among Ammonoids as already shown by him in *Placenticeras*.

The above method of designating the lobes and saddles as paired in the external aspect and on the dorsum on either side of the mesal plane disregards, for sake of convenience, an important fact that should be noted; namely, that the azygous ventral and dorsal lobes are in reality paired with each other in the mesal plane; also that the primitive dorsals and external lateral inflections correspond in the same sense to one another, and are also more or less united across the septa in some forms.

The outlines of the paired lobes and saddles first become complicated in the Carboniferous *Eurycampyli*. Minor or marginal inflections are introduced, and what are termed *bifid* or *trifid lobes* occur in the arms of the ventral (Fig. 1156) lobe; they then affect the primitive first lateral lobes and saddles, and extend thence toward the line of involution (Fig. 1159). These marginal inflections increase greatly in number and complexity during the Permian, become preponderant in the Trias, and universal in the Jura and Cretaceous. During the Carboniferous it is the lobes only, as a rule, that are thus modified; but in the Permian the saddles too are generally affected. The modifications in outline proceed from the lobes to their sides, and thence to the saddle bases, except in certain cases when direct division of the saddles takes place by the outgrowth of secondary median lobes that divide their bases. All these secondary lobes and saddles are termed *marginals*.

Siphuncle.—The caecal condition of the siphuncle is apparently confined to the ananepionic stage or first septum, but J. P. Smith has shown that some species of *Lytoceras* and *Phylloceras* have a bulbous enlargement of this organ, which may persist in several nepionic camerae. This is apparently a persistent remnant of the caecal enlargement. The siphuncle of all Ammonoids is larger

in proportion to the volution, and apt to be nearer the centre (Figs. 1100, 1101) during the young than at later stages, and is also monochoanitic, as in Nauti-

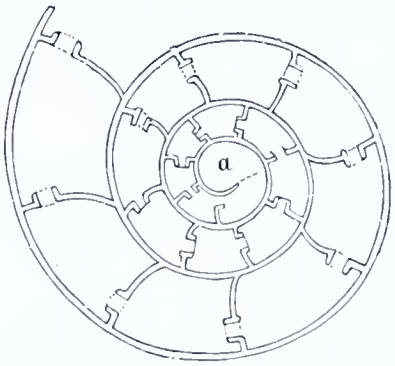


Fig. 1100.

Tropites, cf. *Phoebus*, Dittm. Trias. Enlarged section in the median plane of the young, showing monochoanitic funnels in nepionic stage, then transitional, and later chloiochoanitic funnels. *a*, Position of protoconch (after Branco).

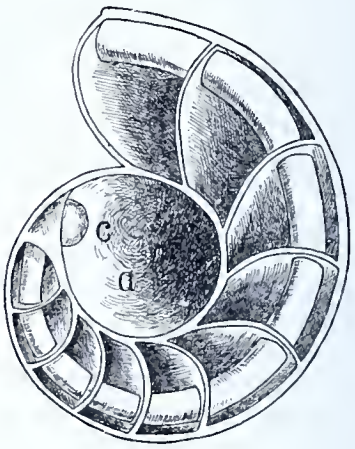


Fig. 1101.

Paltopleurocerasspinatum, Brug. Lias. Section parallel to median plane, showing position of the siphuncle (after Branco).

loids. It remains monochoanitic (having only a funnel) in the *Gastrocampyli*, *Microcampyli*, and *Mesocampyli*, as well as primitive forms of *Eurycampyli;* but it becomes diplochoanitic (having both funnels and forwardly directed collars) in more specialised Carboniferous *Eurycampyli*, and finally chloiochoanitic (funnels lost, collars alone remaining) in Permian genera. Most Triassic and all Jurassic and Cretaceous genera have the siphuncle chloiochoanitic. The above stages are repeated in regular succession during the ontogeny of chloiochoanitic forms (Fig. 1100) except when accelerated development (*tachygenesis*) occurs, and then the monochoanitic stage may disappear. The reduction in size of the siphuncle among Ammonoids is obviously correlated with loss of functional importance, as is also the case among more specialised Nautiloids; and consequently organic deposits are not found in the camerae of these shells.

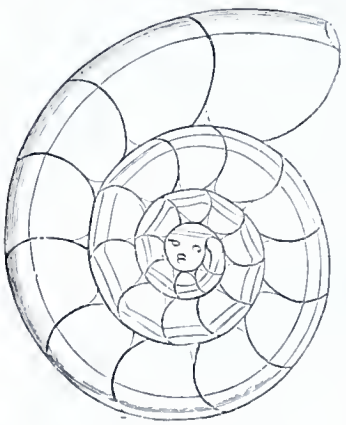


Fig. 1102.

Parkinsonia Parkinsoni, Sowb. Middle Jura. Median section showing siphuncle with bulbous enlargement (*c*), prosiphon (*p*), and position of protoconch (*a*), (after Munier-Chalmas).

Living Chamber.—This varies greatly in all of its dimensions, thus indicating differences in the size and proportions of the animal, since its body parts were probably wholly contained within this cavity. The lines of growth and the few apertures known among *Microcampyli* and *Gastrocampyli* show that they had hyponomic sinuses on the venter, and were swimmers like Nautiloids. The same was probably true of the *Mesocampyli*, except during the gerontic stage of some species when a ventral crest arises, as demonstrated by Clarke. In the *Eurycampyli* and *Glossocampyli* many species that retain the so-called goniatitic form have hyponomic sinuses, but occasionally short ventral crests appear, and later these become general. Only radical Palaeozoic forms of the

Phyllocampyli have retained the hyponomic sinus; short obtuse crests appear in the Trias, and continue thereafter. Jurassic and Cretaceous Ammonoids have as a rule more pointed rostra than those of the Trias, and frequently develop lateral crests and lappets (Figs. 1103-1107).

Very decided decrease in the dimensions of the living chamber during the senile stage does not occur as a rule among Palaeozoic forms; but this condition appears among the Triassic *Haloritidae* and *Tropitidae* with a corresponding contraction of the aperture. The *Arcestidae* (Fig. 1164) and some species of *Discocampyli* also often have very narrow openings during the parageronticsub-stage, but the condition is in no sense phylogerontic except in *Lobites*, and the like (Figs. 1160, 1161).

Pompeckj, in an important essay, asserts that contracted living chambers are invariably developed in old age, and that small shells possessing them are consequently not immature individuals, but dwarfs (Fig. 1107). It is probable that large numbers of shells are indeed dwarfs, but it is also a fact that contraction of the living chamber and volutions occurs in some forms during comparatively early stages; and sometimes in such a way as to affect the ephebic stages of the ontogeny, when the forms become truly *phylogerontic*. This latter term is used to designate shells in which the ontogeny has become permanently modified by the assumption of retrogressive characters that were introduced first in the senile stages of allied progressive species. Whether these peculiar forms have contracted apertures in their earlier stages, and then resorb them before building further, or whether they never add lateral lappets, rostra, etc., as claimed by Pompeckj, until the last resting stage of the ontogeny (Fig. 1107), it is obvious that they are permanently affected by phylogerontic characters.

Fig. 1103.

Dipoloceras cristatum, Deluc. sp. Gault. Aperture with ventral rostrum.

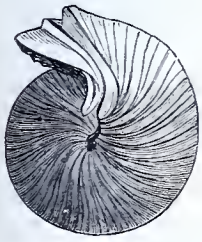


Fig. 1104.

Sphaeroceras Brongniarti, Sowb. sp. Oolite. Aperture with broad, contracted ventral rostrum.

Fig. 1105.

Normannites Braikenridgi, Sowb. sp. Oolite. Aperture with lateral lappets.

Fig. 1106.

Glochiceras nimbatum, Opp. sp. Jura. Lateral lappets.

Fig. 1107.

Oecoptychius refractus, de Haan sp. Jura. Living chamber contracted, with rostrum and lappets.

These forms are comparatively rare in the Trias (*Lobites*, *Cochloceras*), but their number is sensibly increased in the Jura, although usually confined to special localities. During the Cretaceous they become more numerous and

more widely distributed (Figs. 1229-1231). In their extreme modifications they become more or less uncoiled and finally perfectly straight.

Crick and Waagen maintain that Ammonoids had an annular band as well as shell muscles, and that these served both to hold the animal in the living chamber, and also formed an air-tight band around the face of the mantle, fastening the latter to the shell (Fig. 1108). Such was, however, probably not the only means of attaching the animal to the shell. The steady progressive complication of sutures, affecting both lobes and saddles as well as their marginal inflections, is directly correlated with the outgrowth of rostra. The presence of a rostrum indicates the disuse and disappearance of the swimming organ (*hyponome*), which in *Nautilus* causes the formation of the hyponomic sinus in the aperture, and flexed growth-lines on the venter. These facts and the gregarious littoral habits of Ammonoids show that they probably crawled along the bottom with their shells carried above them, very rarely swimming. Their shells are also less bulky in proportion than those of Nautiloids, and correspondingly less buoyant.

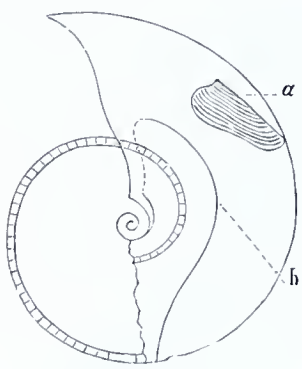


Fig. 1108.

Oppelia steraspis, Opp. sp. Upper Jura; Solenhofen. Compressed shell with aptychus (*a*) preserved in living chamber and distinct impression of shell muscles (*h*), (after Waagen).

All these observations justify the hypothesis that the progressive complication of Ammonoid sutures took place because of their utility in helping to carry and balance the shell above the extruded parts when the animal was crawling. The greater complication of the marginals in Jurassic Ammonoids, where the number of auxiliary lobes and saddles is often reduced (Fig. 1192), and the multiplication of the principal inflections in *Pseudoceratites* of the Cretaceous in compensation for the suppression of marginals (Fig. 1224), are all accounted for by this theory. The phylogerontic forms, in which the lobes and saddles are sometimes reduced in number, and the marginals also less complex—together with the position, form, and mode of growth of the last volution, and the short rostra—suggest that these creatures could not have been active crawlers during the greater part of their ontogeny.

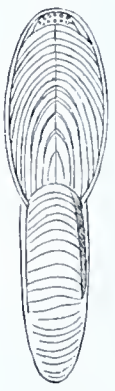


Fig. 1109.

Oppelia subradiata, Sowb. Inferior Oolite; Dundry. Aptychus in place, closing aperture (after Owen).

Fig. 1110.

Aptychus lamellosus, preserved as in Fig. 1108. Upper Jura; Solenhofen, Bavaria.

The occurrence of broods of young shells in the living chamber may be taken as suggesting that some Ammonoids were viviparous, but the examples of this are too rare to be relied upon for making a general statement.

Operculum.—Plates have been found *in situ* closing the aperture and corresponding in position to the hood of *Nautilus* in a number of Ammonoid shells (Fig. 1109). This positive fact, and the obvious fitness of such plates to serve as opercula, lead to the inference that they were formed by an organ

similar to the hood of *Nautilus*, and protected the animal when it was retracted into the living chamber. When composed of a single piece, the plate is called an *anaptychus;* in such cases it is invariably carbonaceous, and was doubtless horny in the living animal (Fig. 1111). The anaptychus is rare in the Palaeozoic, and has not yet been found in the Trias, but occurs among the *Arietidae* and *Amaltheidae* of the Lower Jura. The operculum, when formed of two plates, is termed an *aptychus*, and is always of calcareous composition. It is noteworthy that these plates occur uniformly in the same position among some species from certain localities, inside the living chamber and close to the venter (Figs. 1110, 1112), a circumstance that led Waagen to suppose they served to protect the nidamental gland of female shells. As shown by Michael in *Oppelia*, even the embryonic shells were furnished with aptychi.[1]

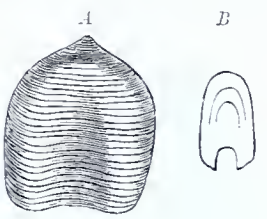


Fig. 1111.

Anaptychi. *A*, *Amaltheus spinatus*, Brug. Lias. 1/1 *B*, *Goniatites Uchtensis*, Keys.

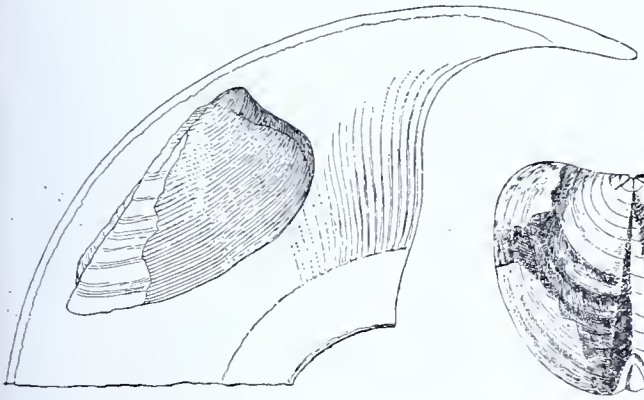


Fig. 1112.

Harpoceras Lythense, Sowb. sp. Upper Lias; Boll, Würtemberg. Aptychus in living chamber.

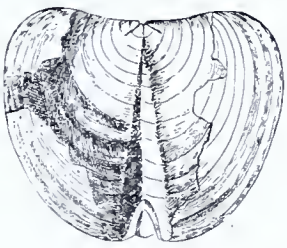


Fig. 1113.

Scaphites spiniger, Schlüt. Upper Cretaceous; Coesfeld, Westphalia. Detached aptychus.

Aptychi are composed of three layers, of which the middle one is the thickest and exhibits a cellular structure, whereas the two outer layers are comparatively dense (Fig. 1115). Detached aptychi have been classified by Zittel into several groups according to their structure. *Cellulosi* (Fig. 1114) are smooth, thick plates, with punctate external surface; *Imbricati* (Fig. 1110) have the surface traversed by oblique folds or costae; *Punctati* (Fig. 1115, *C*) have rows of punctae and overlapping folds; *Granulosi* include thin plates having the external surface covered with concentric folds or rows of tubercles or spinules; *Rugosi* are thick plates with irregularly arranged granules or rows of nodes on the outer surface; *Nigrescentes* (Fig. 1112) are covered with a thin

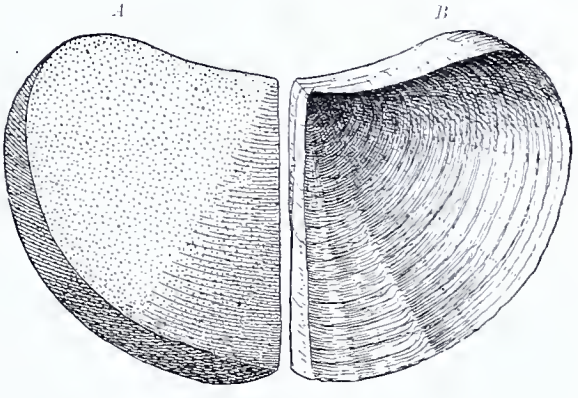


Fig. 1114.

Aptychus laevis, v. Meyer. Lithographic Slates; Solenhofen, Bavaria. *A*, External aspect; *B*, Internal, 1/1.

[1] *Michael, R.*, Zeitschr. deutsch. geol. Ges., XLVI. p. 697, 1894.—*Retowski, O.*, Neues Jahrb., II. p. 220, 1891.—*Blackmore, H. P.*, Geol. Mag. [4], III. p. 529, 1896.

carbonaceous coating; and *Coalescentes* (Fig. 1113) have the two thin plates

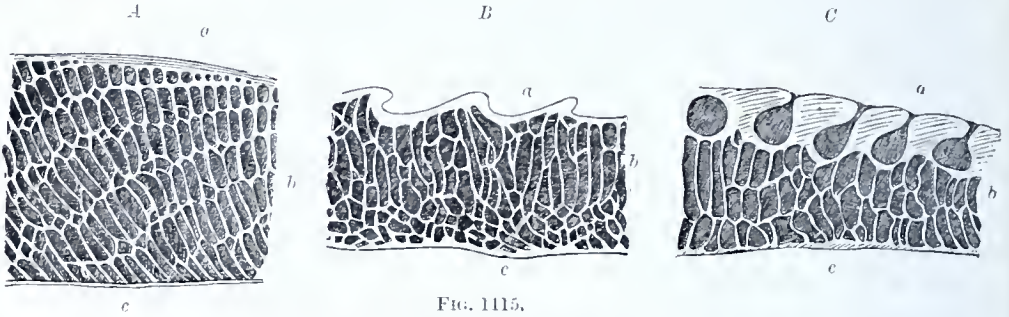


Fig. 1115.

Vertical sections of aptychi belonging to *A*, *Cellulosi* (*A. zonatus*, Stopp.); *B*, *Imbricati* (*A. profundus*, Voltz); and *C*, *Punctati* (*A. punctatus*, Voltz). $^{3}/_{1}$ (after Meneghini and Bornemann).

fused along a median depression. This last is a phylogerontic condition of the aptychus occurring in *Scaphites*.

Classification.—Leopold von Buch prepared the way for a general classification of the *Ammonoidea* by pointing out three grand divisions which he called "genera." These were the Palaeozoic *Goniatites*, *Ceratites*, from the Trias and Cretaceous, and *Ammonites*, from the Jura and Cretaceous. von Buch's chief distinctions were based on the outlines of the lobes and saddles, and were as natural and well-founded as the knowledge of the time permitted. d'Orbigny, Quenstedt, Sandberger, and Barrande greatly increased our knowledge of structure and variation, and defined a number of new genera.

The next marked epoch dates from the publication of Mojsisovics's great works on the Trias, which made known a fauna as rich and complex as that of the Jura. Suess, Neumayr, Branco, Waagen, Buckman, Grossouvre, Haug, Diener, Douvillé, Kilian, Zittel, Karpinsky, the present writer, and others made advances of essential importance along different lines. All of these authors attempted to trace phylogenetic histories which of necessity crossed the lines of the older classifications at right angles, and sometimes bridged over the divisions of geologic time.

All classifications have necessarily been based upon sutural peculiarities. That which is put forward below differs mainly in that it attempts to divide Ammonoids into a number of sub-orders, named with reference to peculiarities of the saddles,[1] and lays special stress upon the phylogenetic significance of the dorsal and internal sutures, especially the antisiphonal lobe. Although some extensive changes are proposed, the system is in reality only a modification of the older schemes, as will be seen from an inspection of the following table. The latter is intended to facilitate comparisons between the primary divisions formerly recognised and the new sub-orders, which are assembled by means of brackets on the left into four corresponding groups.

[1] The suffix *campylus*, signifying curve, in the names of the sub-orders, is used wholly with reference to the saddle inflections as they appear in the typical forms of each group. The term "Pseudoceratites," as used above, is a descriptive expression for the *Placenticeratida* and *Tissotidae* of the Cretaceous, which are morphic equivalents of some Triassic genera of the *Discocampyli* as regards both sutures and shell form. Their origin is traceable, however, to different groups of the *Pachycampyli*, a sub-order which appears to have been initiated in the Jura along with the *Leptocampyli*. It is therefore improbable that the Pseudoceratites were directly connected with the Triassic *Discocampyli*.

TABLE SHOWING PRINCIPAL DIVISIONS OF THE AMMONOIDEA.

	New Sub-Orders.		Equivalents under Former Systems.
Intra-siphonata, Zittel.	*Gastrocampyli*	I.	*Clymenia*, *Clymenidae* (Clymenioids). Characters same as sub-order. Devonian.
Extra-siphonata, Zittel.	*Microcampyli* *Mesocampyli* *Eurycampyli* *Glossocampyli*	II.	*Goniatites*, *Goniatitidae* (Goniatitoids). Zygous inflections entire only in simple or radical forms, becoming divided and similar to Ceratitoids only in some highly specialised genera of the Permian and Trias. The young are asellate in radical forms, becoming latisellate in more specialised genera. Mostly Devonian and Carboniferous; comparatively few Permian representatives.
	Discocampyli	III.	*Ceratites*, *Ceratitidae* (Ceratitoids). Zygous inflections entire only in a few radical forms, probably derived from the same radicals as the *Phyllocampyli*. Lobes become divided by fine marginals forming serrations, but bases of saddles remain entire except in highly specialised genera. Supposed to be mostly latisellate, becoming angustisellate in specialised forms. Triassic.
	Phylloeampyli *Leptocampyli* *Pachycampyli*	IV.	*Ammonites*, *Ammonitidae* (Ammonitoids). Zygous inflections entire only in Palaeozoic radicals of the *Phyllocampyli*. Lobes become divided by fewer and larger marginals than in Ceratitoids; bases of saddles remain entire only in simpler forms of the Triassic *Phyllocampyli*. All others have completely divided inflections except some of the degraded *Pachycampyli*. *Phyllocampyli* range from Devonian to Cretaceous. The last two sub-orders are Jurassic and Cretaceous.

Sub-Order A. GASTROCAMPYLI. Hyatt.

Conchs varying from forms like Anarcestes to those that are more or less compressed in section, and from completely discoidal to compressed and highly involute shells, the surface being either smooth or with large spines. The characteristic ventral saddles are almost imperceptible in some primitive species, and although entire and large as a rule, are in some genera divided by entire ventral lobes. Septa concave along the mesal plane. Siphuncle dorsally situated. Living chamber occupying about three-fourths of a volution; aperture with hyponomic sinus.

The ventral saddles are developed by the obliteration of primitive ventral lobes and fusion of the first pair of saddles (Branco). It is at present questionable whether the ventral lobes of some genera are secondary modifications or retentions of the primitive ventrals, and also whether these can be regarded as divided ventrals even in the *Cymaelymenidae*. The antisiphonal lobe is large and long, and often fused with the siphuncular funnels, which are long and single (*monochoanitic*). The dorsal sutures, so far as known, are very peculiar, having only a pair of large saddles confluent with the last pair of external saddles; or one pair of zygous saddles, and one pair of zygous lobes, the second pair of zygous saddles being confluent with the innermost external pair.

The perforation through the umbilicus, so constant in Nautiloids, is absent, and so too are the umbilical depressions on either side of the neck of the protoconch, common in other Ammonoids. The forms are nevertheless ammoniticones, having the protoconch and other characters of the order. The first septum is described as asellate (Branco), but figured as having a broad saddle on the venter.

Family 1. **Clymenidae**. Gümbel (*emend*). Primitive forms similar to *Anar-*

cestes, but differing in that the sutures have broad entire ventral saddles and broad rounded lobes; or if the latter are angulated, they are incomplete internally, rising to saddles at the lines of involution. Siphuncle tubular and small, and funnels comparatively short (Gümbel).

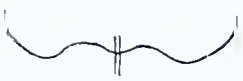


Fig. 1116.

Suture-line of *Cyrtoclymenia lacvigata*, Münst. sp.

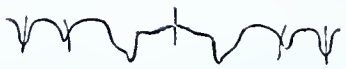


Fig. 1118.

Suture-line of *Cymaclymenia striata*, Münst. sp.

Cyrtoclymenia (Fig. 1116), *Oxyclymenia* (Fig. 1117), Gümbel; *Platyclymenia*, Hyatt. Devonian.

Family 2. **Cymaclymenidae.** Gümbel (*emend*). Conchs similar to those of preceding family, but sutures have two pairs of lateral saddles, and there is a ventral lobe with a median saddle.

Cymaclymenia (Fig. 1118), *Sellaclymenia*, Gümbel. Devonian.

Family 3. **Gonioclymenidae.** Conchs differ from preceding families in that

Fig. 1117.

Oxyclymenia undulata, Münst. sp. Upper Devonian; Elbersreuth, Fichtelgebirge.

Fig. 1119.

Gonioclymenia speciosa, Münst. sp. Upper Devonian; Schübelhammer, Fichtelgebirge. 1/2.

the sutures have deep undivided ventral lobes, and sometimes two pairs of lateral saddles are present. These last may be either in part or wholly divided by marginals.

Gonioclymenia (Fig. 1119), *Cycloclymenia*, *Discoclymenia*, Gümbel; *Cryptoclymenia*, Hyatt; *Acanthoclymenia*, gen. nov. Type *A. (Clym.) neapolitana*, Clarke sp. Devonian.

Sub-Order B. MICROCAMPYLI. Hyatt.

Bactriticones, mimoceracones, and ammoniticones. Sutures entire, and have slight undivided lobes on the venter, and but one pair of broad, shallow lateral lobes in primitive forms. Antisiphonal lobe absent in these, and the dorsal suture has a median saddle, but this becomes divided by a small antisiphonal lobe in some forms. In more specialised shells (Pinnacites) the lateral lobes become divided into two pairs and the dorsal saddles disappear, being replaced by two corresponding lobes, and the septa become at the same time biconcave. Siphuncle subventran, and apparently without calcareous sheath. Funnels narrow, monochoanitic, often long, but never perfectly holochoanitic. Ventral lobes V-shaped, and remain undivided so far as known. Aperture with hyponomic sinus.

Family 1. **Bactritidae.** Bactriticones and cyrtoceracones, usually compressed elliptical in section, and connecting through *Protobactrites* with the *Nautiloidea*.

Bactrites, Sandb. (Fig. 1120). In this, the only genus, the shell is straight, gradually tapering, and round or compressed elliptical in section. Devonian.

Family 2. **Nautilinidae**. (*Nautilini*, Beyrich, *pars*). Mimoceracones and ammoniticones, rounded or more or less quadrangular in section. Sutures have narrow saddles on either side of the undivided ventral lobe, and broad lateral lobes with saddles at the lines of involution or on the umbilical zones, when the latter are differentiated. Antisiphonal lobe absent. Dorsum with a broad azygous saddle. Aperture with a deep and narrow hyponomic sinus, crests on the ventro-lateral angles, and broad lateral sinuses on either side.

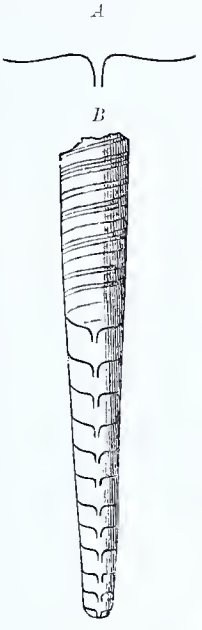


Fig. 1120.

Bactrites elegans, Sandb. Upper Devonian; Büdesheim, Eifel. *A*, Conch, 1/1. *B*, Suture-line, 3/1 (after Sandberger).

Fig. 1121.

Mimoceras compressus, Beyr. sp. Lower Devonian; Wissenbach, Nassau. *A*, *B*, Natural casts, 1/1. *C*, Nepionic individual enlarged.

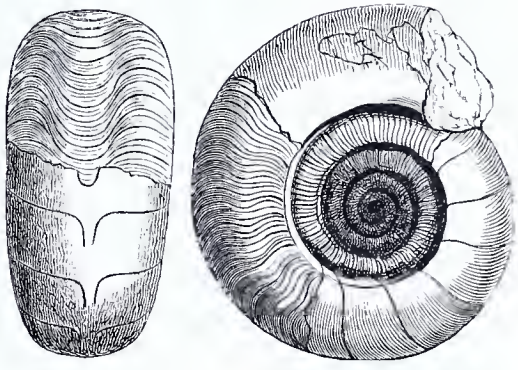


Fig. 1122.

Anarcestes plebejus, Barr. sp. Lower Devonian (Étage G); Hlubocep, Bohemia (after Barrande).

Mimoceras, Hyatt (Fig. 1121); *Anarcestes*, Mojs. (Figs. 1122, 1123); *Prolobites*, Karp.; *Agoniatites*, Meek (*Aphyllites*, p.p. Mojs.), (Fig. 1124); *Palaeogoniatites*, gen. nov. Type *P.* (*Gon.*) *lituum*, Barr. sp. Devonian.

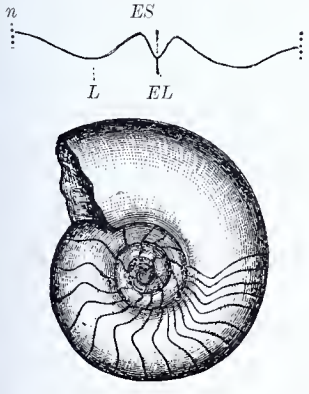


Fig. 1123.

Anarcestes subnautilinus, Schloth. sp. Middle Devonian; Wissenbach, Nassau (cf. Fig. 1094).

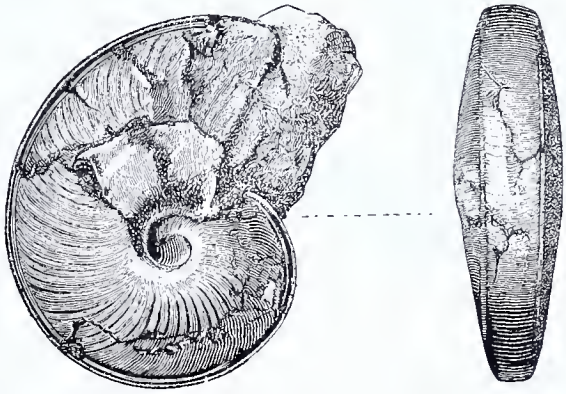


Fig. 1124.

Agoniatites occultus, Barr. Lower Devonian (Étage G); Hlubocep, near Prague, Bohemia (after Barrande).

Family 3. **Aphyllitidae**. Frech. Ammoniticones with truncated venters. Sutures similar to those of *Nautilinidae*, except that a dorsal azygous lobe is present.

Aphyllites, Mojs. Type *A. ambigena*, Mojs. Dorsal sutures unknown. *Paraphyllites*, gen. nov. Type *P.* (*Gon.*) *tabuloides*. Dorsum of this involute form is

entirely occupied by a large azygous lobe terminating in a minute annular lobe and partial cone similar to that observed in Nautiloids and *Pinnacites*. The inner extension or cone is not present elsewhere among Ammonoids so far as known. Devonian.

Family 4. **Pinnacitidae**. Highly involute, compressed ammoniticones with acute venters. Septa biconcave, owing to division of the lateral lobes by narrow saddles which are connected by ridges with corresponding saddles on the dorsum. There are also saddles at the umbilical angles and on either side of the ventral lobes. The azygous dorsal lobe is large and similar to that of *Aphyllitidae*. Dorsum with one pair of narrow zygous saddles and one pair of broad zygous lobes, giving a formula of eight lobes and eight saddles.

Includes only *Pinnacites*, Mojs., from the European Devonian.

Sub-Order C. MESOCAMPYLI. Hyatt.

A provisional group including a few forms which exhibit a wide range of sutural modifications, as well as certain genera intermediate between the nautiliform Anareestes with concave septa, and the normal Ammonoidea with convex septa and large lateral saddles. Ventral lobes invariably divided; siphonal saddles entire in some primitive genera and in a few sporadic forms among the more specialised species. Aperture with hyponomic sinus during the later stages of ontogeny, but in some forms a ventral crest appears during the parageruntic stage (Clarke).

The external sutures sometimes approximate to those of *Anarcestes*, but the dorsals have only one large azygous lobe, the saddle being confluent at the line of involution with the second external pair. In more involute forms the antisiphonal lobe is large, entire, and pointed; there is one pair of dorsal saddles, and one of broad dorsal lobes; the second pair of saddles, when present, is confluent with the second pair of lateral saddles.

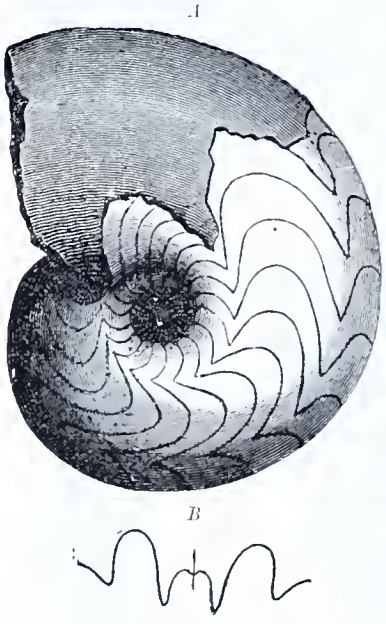


Fig. 1125.

Gephyroceras intumescens, Beyr. Upper Devonian; Nassau. *A*, Conch, 1/1. *B*, Suture-line.

Family 1. **Neoicoceratidae**. This includes the unique *Neoicoceras*, gen. nov., which combines the lateral sutures of *Anarcestes* with the divided ventral lobes of the *Primordialidae*, but the siphonal saddles are large and entire. Volutions discoidal and trapezoidal in section, similar to the young of *Gephyroceras calculiforme*, Sandb. sp. Position of siphuncle unknown. Type *P.* (*Gon.*) *elkhornensis*, Mill. and G. sp. Carboniferous; Illinois.

Family 2. **Primordialidae** (*Primordiales*, Beyr.). Distinguished from *Anarcestes* by the divided ventral lobes, large siphonal saddles, and especially the first lateral saddles, which are very prominent on the sides. Adventitious lobes and saddles are formed by division of the first lateral saddles. Septa in the young concave and similar to those of *Anarcestes*, but in later stages become convex along the mesal plane as in normal Ammonoids. Siphuncle small, subventran, without calcareous sheath; funnels monochoanitic and short.

Gephyroceras (Fig. 1125), *Manticoceras*, Hyatt; *Probeloceras*, Clarke; *Timanites*, Mojs. Devonian. *Milleroceras*, gen. nov. Type *M.* (*Gon.*) *Parrishi*, Mill. and G. sp. Upper Coal Measures; Illinois.

Sub-Order D. EURYCAMPYLI. Hyatt.

Conchs varying in primitive genera from forms like Anarcestes to highly coronate with entire lobes and saddles. The ventral and lateral lobes become divided in specialised Palaeozoic genera, and the more highly specialised Permian and Triassic forms have the lobes and saddles completely divided. The large inner saddles characteristic of the ephebic stage of Magnosellaridae are retained throughout life in many Palaeozoic forms, and occur more or less in the young of Triassic genera. Among the latter the coronate form of Gastrioceras is also common.

I. Magnosellarida.

Prevailing form of conch Anarcestes-like, but sometimes discoidal, and more or less quadrangular or trapezoidal in section. Sutures entire, with large inner lateral saddles resembling those of Glyphioceras in most Palaeozoic forms, but the lobes become more digitated in some Carboniferous and Permian genera, and both lobes and saddles are completely divided in highly specialised Triassic genera. Ventral lobe undivided in primitive forms, but split by a siphonal saddle which is in turn subdivided by minute funnel lobes in the more specialised species. Siphuncle without calcareous sheath; funnels monochoanitic in primitive forms, and diplochoanitic or sometimes even chloiochoanitic in specialised Permian forms.

Primitive genera have deep undivided antisiphonal lobes and only one pair of large broad dorsal saddles; the first pair of lobes, when present, are confluent with the second lateral lobes at the lines of involution. More specialised shells may retain a pointed undivided antisiphonal, but the dorsals may have one pair of entire narrow saddles, one pair of entire pointed lobes, and usually a second pair of saddles. These last are broad, similar to the lateral pair, or confluent with the third laterals when there is a third external pair.

Family 1. **Magnosellaridae.** Beyrich. Ammoniticones varying from discoidal and *Anarcestes*-like to highly involute, compressed shells with narrow venters. Septa concave along the mesal plane as in Nautiloids, becoming convex only internally and laterally, following the broad internal saddles in the zone of involution. Lobes and saddles entire. Primitive forms may have only two broad saddles on either side, but more specialised shells may have two pairs of principal saddles formed by division of the primitive first laterals. There is a corresponding development of narrow saddles and lobes on the dorsum, but primitive forms have only two broad saddles here as in *Anarcestes*. Antisiphonal lobe narrow, entire, pointed. Aperture with hyponomic sinus. Shells smooth.

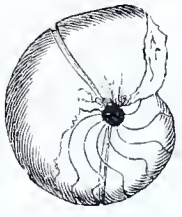


Fig. 1126.

Tornoceras retrorsus, v. Buch. Upper Devonian; Büdesheim, Eifel. 1/1.

Fig. 1127.

Tornoceras simplex, v. Buch. Upper Devonian; Büdesheim, Eifel.

Fig. 1128.

Suture-line of *Sporadoceras Münsteri*, v. Buch. sp.

Fig. 1129.

Suture-line of *Maeneceras terebrutus*, Sandb. sp.

Parodoceras (*Cheiloceras*, Frech); *Tornoceras* (Figs. 1126, 1127), *Sporadoceras* (Fig. 1128), *Maeneceras*, Hyatt (Fig. 1129); *Paratornoceras*, gen. nov. Type *P.* (*Gon.*) *lentiforme*, Kayser sp. *Goniolobоceras*, gen. nov. Type *G.* (*Gon.*) *goniolobus*, Meek sp. *Pseudoclymenia*, Frech. Devonian and Carboniferous.

Family 2. **Pericyclidae.** Involute shells resembling *Glyphioceratidae*, but having

the broad inner lateral saddles divided by a pair of shallow lobes into two nearly equal saddles. Ventral lobe in primitive *Dimeroceras* undivided, and this together with the sutures indicates common ancestry with *Brancoceras* and *Magnosellaridae*. Aperture with broad shallow hyponomic sinus. Shells have annular costae crossing the venter.

Dimeroceras, Hyatt; *Pericyclus*, Mojs. Devonian and Carboniferous.

Family 3. **Glyphioceratidae**. Ammoniticones of variable form, including discoidal and highly involute shells, and also a large proportion of *Anarcestes*-like genera. Septa concave along the mesal plane in primitive *Brancoceras*, but becoming convex as a rule along this plane in the later stages of other genera. Ventral lobe entire in primitive forms, but becoming divided in more specialised genera. External sutures similar to those of *Magnosellaridae*, but dorsal sutures have narrow saddles on either side of the entire pointed antisiphonal lobe.

Fig. 1130.

Suture-line of *Brancoceras sulcatus*, Münst. sp. Upper Devonian; Fichtelgebirge.

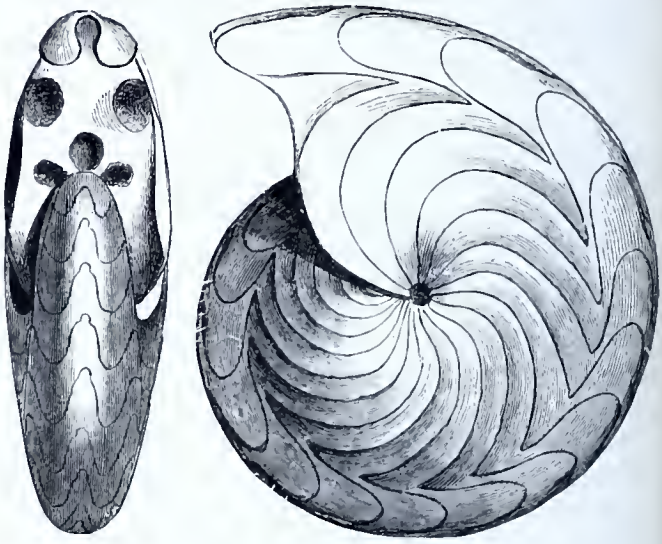


Fig. 1131.

Brancoceras rotatorius, de Kon. sp. Carboniferous Limestone; Tournay, Belgium.

Siphuncle small, and funnels generally diplochoanitic, except in species with undivided ventral lobes. Aperture usually with hyponomic sinus, but some species have ventral crests during ephebic stages. Shells smooth, tuberculated or costated, but costae do not cross the venter as a rule. Venter sometimes with well-marked longitudinal ridges.

Fig. 1132.

Gastrioceras Jussae, M. V. K. Permo-Carboniferous; Artinsk, Ural.

Fig. 1133.

Glyphioceras sphaericus, Goldf. sp. Carboniferous Limestone; Suttrop, Westphalia.

Brancoceras (Figs. 1130, 1131); *Muensteroceras*, *Gastrioceras* (Fig. 1132), *Glyphioceras* (Figs. 1133, 1134), *Paralegoceras*, *Schistoceras*, Hyatt; *Pronannites*, Haug. Devonian and Carboniferous.

Fig. 1134.

Glyphioceras diadema, Goldf. sp. Carboniferous Limestone; Choquier, near Liège, Belgium.

Family 4. **Dimorphoceratidae**. Discoidal compressed shells; primitive species like *Prolecanites*, but specialised forms are more or less involute, although still retaining modified Anarcestean aspect. Lobes become digitated, beginning with the arms of the ventral lobe and progressing inwards, but bases of saddles remain entire. The broad undivided saddles of *Magnosellaridae* are

represented in primitive species, and are more or less traceable even in specialised shells. Aperture with hyponomic sinus. Shells smooth or with longitudinal grooves.

Examples: *Dimorphoceras*, *Nomismoceras*, Hyatt. Carboniferous.

Family 5. **Thalassoceratidae.** Discoidal and involute ammoniticones with undivided ventral lobes in primitive forms, and also entire lobes and saddles; but in more specialised shells the former are divided, and the latter digitated by marginals, but bases of saddles may remain entire. Outlines of sutures in primitive forms indicate affinity with *Nomismoceras*, and probable derivation from same stock. Aperture with hyponomic sinus. Shells smooth.

Examples: *Paraceltites*, *Thalassoceras*, Gemm. Permian.

II. Nannitida.

A provisional group, including smooth, more or less discoidal and globose keelless forms with primitive sutures. The latter pass through a Magnosellarian stage in the young, but subsequently assume the aspect of Dimorphoceratidae. Ventral lobes retain entire siphonal saddles throughout life. Specialised forms have elevated subacute and often keeled venters.

Family 6. **Nannitidae.** Anarcestean forms with a tendency to become elevated on the venter in later stages of growth, and having sutures with faintly denticulated lobes and entire saddles, and with very small entire siphonal saddles.

Nannites, *Prosphingites*, Mojs. (?) *Sphaerites*, Arthaber. Trias.

Family 7. **Otoceratidae.** Involute forms with deep umbilici and prominent ridged umbilical shoulders; venter keeled and acute. Ventral lobes divided by large siphonal saddles. Young have volutions with broad keelless venter and trapezoidal section. Antisiphonal lobe, so far as known, entire on the sides and bifid at the ends.

Otoceras, Griesbach; *Anotoceras*, gen. nov. Type *A.* (*Prosph.*) *nala*, Diener sp. Trias.

III. Tropitida.

Includes a large and comparatively homogeneous group of Triassic shells of Anarcestes-like aspect, but sutures with peculiarly elongated and completely digitated saddles and lobes. Siphonal saddles not so deeply incised by marginal lobes as the laterals, nor very complex in outline. Shells ornamented with costae, often tuberculated, keeled, and channeled. Aperture invariably with lateral crests. Connects through Microtropites with Nannites.

Family 8. **Tropitidae.** Mojsisovics (*pars*). Similar to *Anarcestidae* in the ephebic stage, but the young frequently have volutions with highly trapezoidal

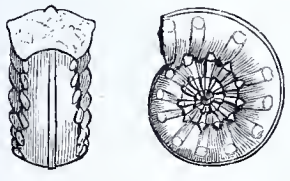


Fig. 1135.

Margarites Jokelyi, Hauer sp. Upper Trias; Sandling, near Aussee, Austria.

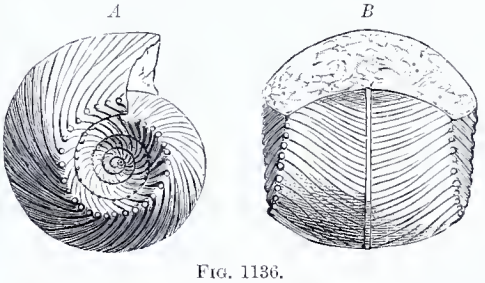


Fig. 1136.

Tropites subbullatus, Hauer sp. Upper Trias; Aussee, Austria. 1/1.

sections. Shells highly ornamented by the intersection of a system of longitudinal ridges and transverse costae. Sutures have deep, narrow ventral lobes divided by siphonal saddles with peculiar truncated bases, which are often retained in later stages. Sutures in ephebic stages of some forms are similar to those of *Haloritidae*; young have a more or less prolonged coronate stage, and are also keeled on the venter as a rule. Aperture narrower and with more pointed ventral crests than in *Haloritidae*.

Margarites (Fig. 1135), *Tropites* (Figs. 1092, *C*, 1100, 1136), (*Paratropites*, *Anatropites*, *Microtropites*), *Barrandeites*, *Silbyllites*, Mojs.; *Eutomoceras*, Hyatt. Trias.

Family 9. **Haloritidae.** Mojsisovics (*pars*). Shells more globose and more involute in the young than *Tropitidae*, and as a rule keelless, but having similar volutions in a number of species during later stages. Ornament as a rule simpler than in *Tropitidae*. Aperture usually with ventral crests, but these are primitive in outline, broad, and in some species scarcely indicated by the lines of growth.

Halorites (*Homerites*), *Jovites*, *Parajuvavites*, *Juvarites* (*Anatomites*, *Griesbachites*, *Dimorphites*), *Miltites*, *Sagenites* (*Trachysagenites*), Mojs. Trias.

Sub-Order E. GLOSSOCAMPYLI. Hyatt.

Primitive species exhibit close resemblance to Prolecanitidae, but differ in the greater number and simpler forms of the tongue-shaped saddles and lobes. Specialised shells have the saddles acute, but still entire and of the same fundamental outlines, while the lobes become bifid or digitated. Adventitious lobes and saddles are introduced by division of the siphonal saddles, and generally show reminiscence of their primitive ancestral outlines. Siphuncle as in preceding groups, devoid of a calcareous sheath; funnels monochoanitic and short in primitive genera (Phareiceras), but becoming chloiochoanitic in specialised forms. Antisiphonal lobe entire in primitive, but bifid in more specialised shells.

Two pairs of entire dorsal saddles and one pair of zygous lobes with rounded outlines appear in *Sandbergeroceras*, but in more involute and specialised genera the dorsal inflections become more numerous; their outlines remain comparatively simple, however, except in *Hedenstroemitidae*. There is a general tendency in this sub-order toward the multiplication of lobes and saddles, and these are added at both external and internal ends of the lateral sutures. The lobes and saddles are less differentiated, or are more alike, than in preceding groups throughout the entire lateral line. The sutures of *Pharcieceras*, however, show the presence of large internal saddles in some species, indicating derivation from *Magnosellaridae*.

Family 1. **Pharciceratidae.** More or less discoidal shells resembling *Anarcestes*, but having the lobes and saddles like those of *Beloceratidae*, with, however, simpler and more rounded outlines. No adventitious inflections are developed. Ventral lobe undivided, and antisiphonal lobes entire. Aperture with large hyponomic sinus.

Pharciceras, *Sandbergeroceras* (*Trianoceras*), Hyatt (Fig. 1137); *Hoeninghausia*, Gürich. Devonian. (?) *Beneckia*, Mojs. Trias.

Fig. 1137.

Suture-line of *Sandbergeroceras tuberculoso-costatum*, Sandb. Upper Devonian.

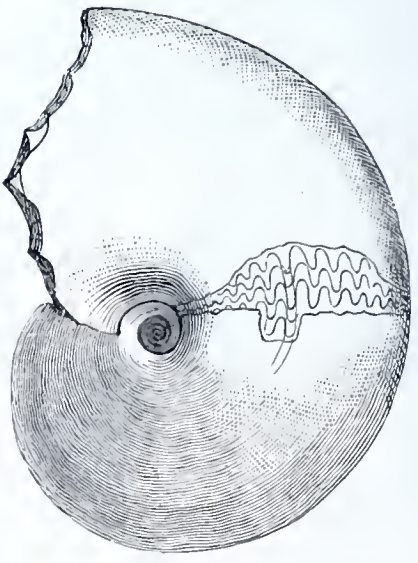


Fig. 1138.

Beloceras multilobatum, Beyr. sp. Upper Devonian; Adorf, Westphalia.

Family 2. **Beloceratidae.** Frech. Includes only the genus *Beloceras*, Hyatt

(Fig. 1138), which is highly involute and compressed, with flat and narrow venter. Sutures with more or less acute lobes and saddles, as well as a number of adventitious and auxiliary inflections. Ventral lobe divided, and funnels monochoanitic. Aperture with hyponomic sinus, and the lateral outlines simpler than in the next family. Devonian.

Family 3. **Sageceratidae.** Similar to the last, but lateral lobes bifid, and saddles acutely spade-shaped. Antisiphonal lobe bifid. Aperture has sinuous lateral outlines with crests at the ventrolateral ridges.

Pseudosageceras, Diener; *Sageceras*, Mojs. (Fig. 1139). Permian and Trias.

Family 4. **Hedenstroemitidae.** Principal lobes and saddles with ceratitic outlines as in *Discocampyli*, but adventitious lobes and saddles have *Sageceras*-like outlines. Antisiphonal lobe bifid and very long. Dorsal inflections more complex than in preceding families. Aperture with ventral crests.

Hedenstroemia, Waagen; *Anahedenstroemia*, gen. nov. Type *A.* (*Heden.*) *Mojsisovicsi*, Diener sp. Trias.

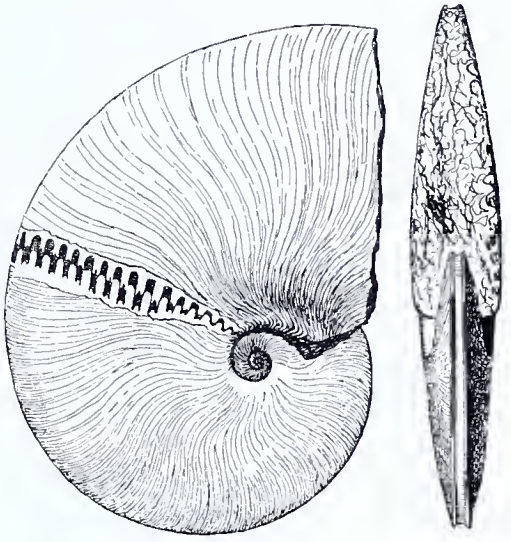


Fig. 1139.

Sageceras Haidingeri, Hauer sp. Upper Trias; Hallstadt, Austria.

Sub-Order F. DISCOCAMPYLI. Hyatt.

Primitive genera show close approximation to primitive types of Prolecanitidae. Bases of saddles retain the entire rounded outlines of Lecanites even in specialised genera, but the lobes become completely divided by fine marginal serrations or digitations. This purely ceratitic outline is maintained more or less in all groups except highly specialised genera, in which the saddles are completely divided and the discocampylic bases disappear. Antisiphonal lobe entire in primitive, but bifid or trifid in specialised forms, and zygous dorsal inflections assume the ceratitic outline in some genera. Ventral lobes very broad and short, and have very broad siphonal saddles in typical forms.

The number of external inflections rarely exceeds three saddles and three lobes in primitive forms, and the first pair of lobes as a rule is very much longer and broader than the others. While the external saddles often assume approximately monophyllic outlines, the dorsal saddles commonly retain the broader and less differentiated aspect of *Lecanitidae*, and saddles never become divided. The number of dorsal inflections is more limited in most forms than in *Phyllocampyli*, and when lengthened by additional inflections, the digitations are apt to be irregular.

I. Lecanitida.

Compressed discoidal and involute forms. Compressed primitive genera have entire sutures with broad rounded saddles and rather narrow lobes, the ventral lobe being broad and shallow, and the siphonal saddle also broad. Involute shells generally have prolonged lateral suture-lines with an indefinite number of often irregularly proportioned inflections, which are really marginals arising from the division of a prolonged inner saddle or nearly straight, depressed lobe-like inner line. Dorsal sutures have similar characters and the antisiphonal lobe, which is entire and pointed in primitive forms, usually remains entire on the sides and bifid at the extremities in specialised forms.

Family 1. **Lecanitidae**. Primitive discoidal shells like those of *Prolecanitidae*, with short rounded entire saddles and lobes like those of *Ibergiceras*, but ventral lobes divided by short, comparatively broad and entire siphonal saddles. There are all stages in the development of these saddles, so that their aspect is rather variable. There are as a rule but two principal lateral saddles and lobes, with one auxiliary saddle and shallow lobe on either side in primitive species, but in others the number of auxiliaries may be considerably increased. Antisiphonal lobe entire, and often long and acute. The zygous dorsal lobes are very slight so far as known, and entire; merely marginals in the dorsal saddles.

Paralecanites, Diener; *Lecanites*, Mojs.; *Kymatites*, *Parakymatites*, Waagen; *Proarites*, Arthaber. Trias.

Family 2. **Badiotitidae**. Discoidal and involute shells similar to *Lecanites*, especially in the dorsal sutures, but with well-defined costae and keeled venters. Includes *Badiotites*, Mojs. (Fig. 1140), and *Doricranites*, Hyatt. Trias.

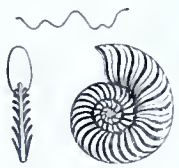


Fig. 1140.

Badiotites Eryx, Münst. sp. Keuper; St. Cassian, Tyrol.

Family 3. **Flemingitidae**. A provisional group of discoidal forms having longitudinal ridges as in *Cladiscitidae*. The characteristics of *Wyomingites* connect it apparently with *Lecanitidae*, while in *Flemingites* the saddles are long and have a monophyllic aspect. There are, however, no truly monophyllic saddles at any stage so far as known. The suture lines do not have the inner extensions common in *Gyronitidae*. Antisiphonal lobe bifid, its sides entire, and zygous dorsal inflections limited in number; but the lobes are very broad, and their marginal saddles pointed, irregular in size.

Xenodiscus, *Xenaspis*, *Flemingites*, Waagen; *Wyomingites*, gen. nov. Type *W.* (*Meekoc.*) *aplanatum*, White sp. Permian and Trias.

Family 4. **Meekoceratidae**. Waagen (*pars*). Shells smooth, compressed, discoidal, and involute, and as a rule with narrow and more or less flattened venter. Sutures in many forms have a tendency to extend the inner lateral saddles or lobes, and to develop a corresponding series of auxiliaries; and this is carried to an excessive extent among some highly involute shells. The ventral lobes, however, are apt to remain broad and shallow; their arms become highly denticulated except in *Gyronites*, where they are narrow and pointed as in *Lecanitidae*. Saddles entire and generally somewhat elongated and linguiform, but plainly of the *Lecanites* type. Antisiphonal lobe, so far as known, long, narrow, and bifid so far as known. Extremities of dorsal sutures produced and corresponding with inner parts of external sutures.

Meekoceras, Hyatt; *Nicomedites*, Toula; *Prionolobus*, *Gyronites*, *Beyrichites*, *Koninckites*, *Kingites*, *Aspidites*, *Proptychites*, *Clypites*, *Paranorites*, Waagen; *Apleurocerus*, gen. nov. Type *A.* (*Ceratites*) *Sturi*, Mojs. sp. Trias.

Family 5. **Prionitidae**. Similar to *Gyronitidae*, but nodes, when they occur, are larger, and sutures have more or less pointed siphonal saddles, which are usually divided by a siphonal lobe. Dorsal sutures, so far as known, have fewer inflections and different outlines.

Ophiceras, Griesb.; *Vishnunites*, Diener; *Prionites*, *Goniodiscus*, Waagen; *Aplococeras*, gen. nov. Type *A.* (*Din.*) *arisianus*, Mojs. sp. *Plococeras*, gen. nov. Type *P.* (*Din.*) *dalmatianus*, Mojs. sp. *Diaplococeras*, gen. nov. Type *D.* (*Din.*) *liccanus*, Mojs. sp. Trias. *Protophiceras*, gen. nov. Type *P.* (*Danub.*) *Nicolai*, Diener. Trias.

11. Aegoceratida.

Apparently connected through primitive forms with Protophiceras, although sutures of later stages in most forms depart widely from the discocampylic outline, and are quite similar to those of Pinacoceratidae. The auxiliary series, however, is highly inclined upicad as a rule, and develops differently. There are no adventitious inflections.

Family 6. **Ptychitidae.** Similar in aspect to primitive forms of *Gyronitidae*, but having subacute venters, less complex sutures, and the auxiliary series straighter, as in *Prionitidae*. *Ptychites* (Fig. 1141), *Japonites*, Mojs.; *Pseudodanubites*, gen. nov. Type *P.* (*Danub.*) *dritarshtra*, Diener sp. Trias.

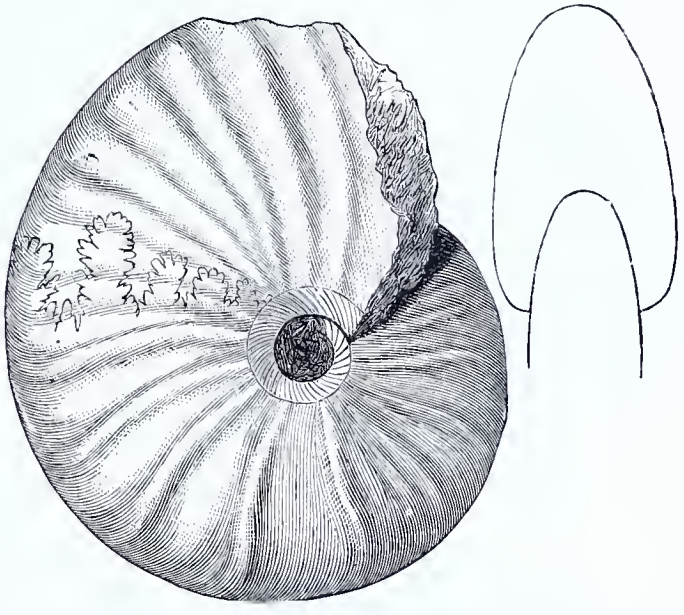


Fig. 1141.

Ptychites flexuosus, Mojs. (=*Amm. Studeri*, Hauer p.p.). Muschelkalk; Schreyer Alp, Salzburg, Austria.

Family 7. **Aegoceratidae.** Neumayr (restrict.). Smooth, compressed, discoidal shells with rounded venter in primitive forms, becoming involute with acute venter in specialised species. Sutures similar in convexity and general aspect to those of *Pinacoceratidae*, but having peculiar, highly inclined auxiliaries which are developed apparently from marginals on the umbilical sides of the saddles; no corresponding adventitious inflections. Siphonal saddle similar to that of *Prionitidae*, and arms of the ventral lobe narrow. First lateral saddles are dependent on, or attached to the large siphonal saddles, and often simulate adventitious saddles.

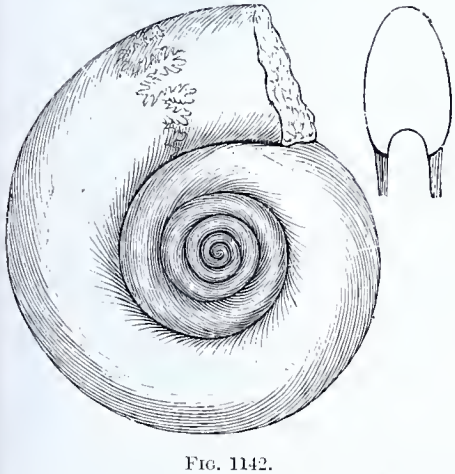


Fig. 1142.

Aegoceras (=*Gymnites*) *Palmai*, Mojs. Muschelkalk; Schreyer Alp, near Gosau, Austria.

Aegoceras, Waagen, s. str. (*Gymnites*, Mojs.), (Fig. 1142); *Buddhaites*, Diener; *Anagymnites*, gen. nov. Type *A.* (*Gym.*) *Lamarcki*, Diener sp. *Paragymnites*, gen. nov. Type *P.* (*Plac.*) *sakuntala*, Mojs. sp. Trias.

Family 8. **Hungaritidae.** Involute forms with keeled or more or less acute venter. Ventral lobes remain undivided in some forms until a late stage of growth. Specialised shells have a more or less extensive series of auxiliaries, and a few adventitious inflections derived from division of the siphonal saddle.

Hungarites, *Carnites*, *Longobardites*, Mojs.; *Noetlingites*, gen. nov. Type *N.* (*Hung.*) *Strombecki*, Griepenk sp.; *Iberites*, gen. nov. Type *I.* (*Hung.*) *Pradoi*, Mojs. sp. Trias.

III. Ceratitida.

Primitive forms discoidal, compressed, and have sutures with undivided ventral lobes; specialised forms have the latter divided, and shells more or less involute, also more or less nodose or costated. Saddles are of the typical discophyllic form, the lobes usually narrow, denticulated, long, and broadening more or less at the apical ends. Ventral lobes in these are apt to be very broad and shallow, with denticulated arms, and small divided siphonal saddles.

Family 9. **Celtitidae.** Primitive forms discoidal, compressed, and costated. The costae in some cross the venter, and are also developed after a tuberculated stage as in *Sibiritidae*. Sutures in these are often entire, the ventral lobe undivided (*Cycloceltites*), and there may be but one pair of principal laterals, or at most two pairs, with one pair of auxiliary lobes. Affinity with *Ibergiceras* and *Lecanitidae* is indicated by the sutures of these shells. Specialised forms have smooth zones or keels on the venter. Antisiphonal lobe entire in primitive genera, becoming bifid in specialised forms and often very long. Costae and all characters, except sutures in some genera (*Arniotites*) approximate closely to Liassic forms.

Cycloceltites, *Celtites*, *Styrites*, *Tropiceltites*, *Arnioceltites*, and perhaps *Haidingerites*,

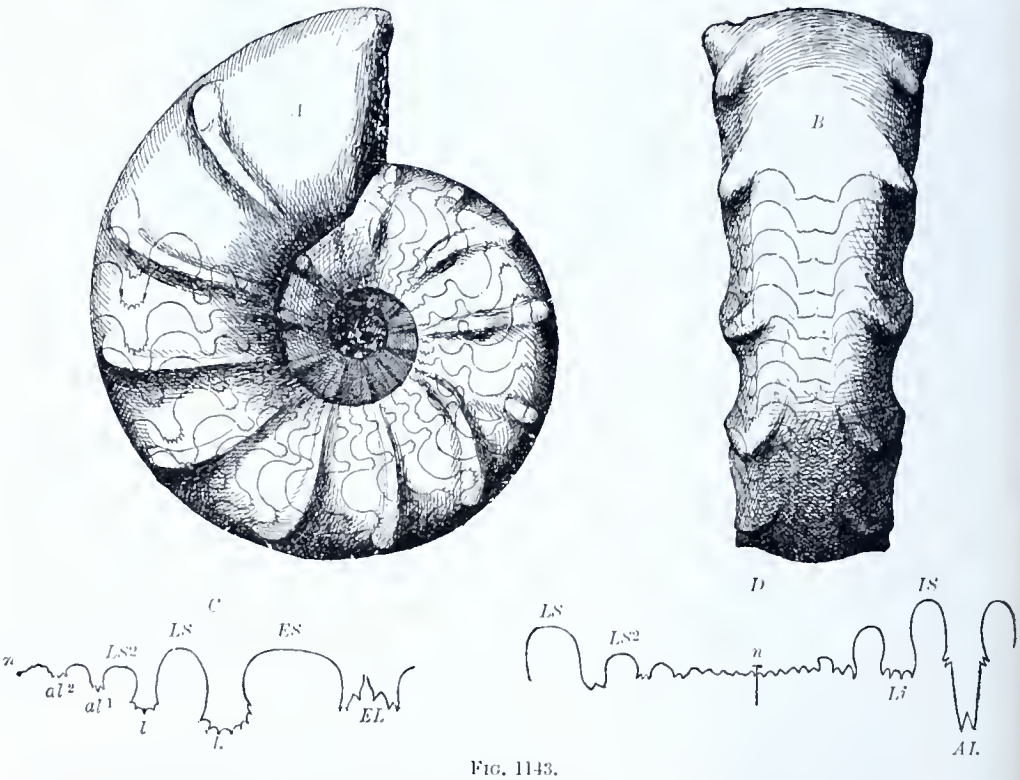


FIG. 1143.

Ceratites nodosus, de Haan. Muschelkalk; Würzburg, Bavaria. *A*, *B*, Conch, 1/3. *C*, Left half of suture-line. *D*, First and second lateral saddles and auxiliaries to left of line of involution (*n*); half of dorsal suture-line to right. (*AL*, Antisiphonal lobe; other lettering as in Figs. 1096-1097.)

Mojs.; *Arniotites*, Hyatt; *Florianites*, gen. nov. Type *F.* (*Celt.*) *Floriani*, Mojs. sp. Trias.

Family 10. **Sibiritidae.** Mojsisovics. Primitive forms discoidal and often tuberculated, giving rise to involute and compressed shells, without tubercles and with slighter costae. The costae usually cross the venter and are often more or less convergent to nodes on the ventro-lateral angles of some shells, which usually have a broad venter and more or less trapezoidal section. The nodes disappear in later stages, when the sides generally become more rounded, and the venter more elevated. Sutures have divided ventral lobes, with divided siphonal saddles. Lateral inflections entire in primitive, but in specialised forms the lobes become denticulated.

Stephanites, Waagen; *Sibirites*, *Anasibirites*, *Metasibirites*, *Thetidites*, Mojs.; *Parastephanites*, gen. nov. Type *P.* (*Achroch.*) *atavus*, Waagen sp. *Pseudoceltites*, gen. nov. Type *P.* (*Celt.*) *multiplicatus*, Waagen sp. Trias.

Family 11. **Ceratitidae.** Mojsisovics (*pars*). Primitive forms discoidal or

involute, but stout-whorled and keelless, becoming more compressed, and having a broad slightly elevated median ventral ridge in more specialised genera. Sides have at least one line of nodes in primitive forms, and are more or less completely costated with several lines of tubercles in specialised shells. Sutures in the young and in primitive genera have a magnosellarian aspect, but when the broad internal saddles become divided, the internal inflections resemble those of Lecanitidae. In primitive forms (*Olenikites*) the saddles are broad and very shallow; lobes entire, and ventral lobe divided by a larviform siphonal saddle, which is sometimes entire.

The large nodes and stout volutions of primitive forms indicate parallelism with *Stephanites* and *Parastephanites* of the preceding family. Saddles and lobes have the typical ceratitic outlines, as a rule, but in some forms the auxiliary line may be extended as in *Gyronitidae*. Occasionally, also, costae may cross the venter as in *Sibiritidae*.

Fig. 1144.

Paraceratites trinodosus, Hauer sp. Muschelkalk; Bakony, Hungary (after Mojsisovics).

Ceratites, Haan (Fig. 1143); *Danubites*, Mojs.; *Balatonites*, Mojs.; *Reiflingites*, Arthaber; *Gymnotoceras*, Hyatt; *Paraceratites*, gen. nov. Type *P.* (*Cer.*) *elegans*, Mojs. sp. (Fig. 1144); *Olenikites*, gen. nov. Type *O.* (*Din.*) *spiniplicatus*, Mojs. sp. *Keyserlingites*, gen. nov. Type *K.* (*Cer.*) *subrobustus*, Mojs. sp.; *Arctoceras*, gen. nov. Type *A.* (*Cer.*) *polaris*, Mojs. sp.

IV. Tirolitida.

Primitive forms compressed, discoidal, and have only one pair of narrow entire lateral lobes, and two broad entire saddles with incomplete lobes in the umbilicus as in Parodoceras. Number of inflections seldom exceeding three or four, and the auxiliary sutures never much extended.

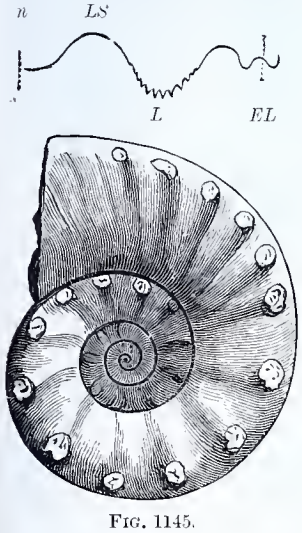


Fig. 1145.

Tirolites Cassianus, Quenst. sp. Upper Trias; Grones-Hof, near St. Cassian, Tyrol.

Family 12. **Tirolitidae.** Mojsisovics (*pars*). Compressed, discoidal, or involute shells resembling *Dinaritidae* in their sutures, and having entire saddles and slightly denticulated lobes. Ventral lobe may remain entire until a late stage in some forms, but as a rule it is divided, and siphonal saddle is small and often entire. Shells have a line of nodes on the ventro-lateral angles, and the venter is invariably smooth and convex.

Includes *Tirolites* (Fig. 1145) and *Metatirolites*, Mojs., from the Alpine Trias. Sub-Family Clydonitinae. Sutures similar to *Tirolites*, but costae interrupted on the venter, which is often channeled. Includes *Clydonites*, *Eremites*, Hauer; and *Ectolcites*, Mojs. Trias.

Family 13. **Dinaritidae.** Mojsisovics (*pars*). Sutures resembling *Tirolites* in having only two broad saddles, one pair of first lateral lobes, and incomplete lobes at the umbilicus. Shells smooth, or with coarse folds most prominent at the umbilical shoulders; sides more or less flattened or plano-convex, and venter rounded.

Dinarites, Mojs. (?) *Pseudoharpoceras*, Waagen; *Pseudodinarites*, gen. nov. Type *P.* (*Din.*) *mahommedanus*, Mojs. sp. Trias.

Family 14. **Buchitidae.** Primitive forms similar to *Celtitidae*, with smooth elevated venter; more specialised shells with slight keel on the narrow venter, and simple costae or folds on the sides. Sutures have entire outlines, or lobes but slightly

denticulated; and when the saddles are completely divided their marginals are small. Sutures otherwise similar to those of Dinaritidae, and the young have a *Dinarites* stage. Antisiphonal lobe entire and bifid in some forms.

Buchites, *Helictites*, *Phormedites*, *Parathisbites*, *Glyphidites*, Mojs., and perhaps *Eudiscoceras*, Hyatt. Trias.

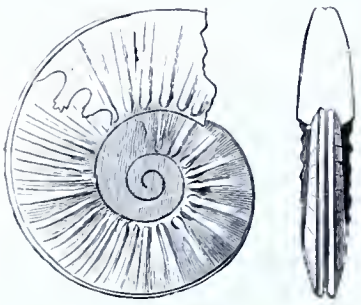


Fig. 1146.

Arpadites Cinensis, Mojs. Keuper; Esino, Lombardy.

Family 15. **Arpaditidae**. Differs from *Buchitidae* in the tendency to form channeled venters bordered by two ridges, which may be either tuberculose or smooth.

Arpadites (Fig. 1146), *Klipsteinia*, *Dittmarites*, *Muensterites*, *Steinmannites*, *Daphnites*, *Dionites*, *Drepanites*, *Heraclites*, *Guembelites*, *Cyrtopleurites*, and *Acanthinites*, Mojs. (?) *Bosnites*, Hauer. Trias.

Family 16. **Trachyceratidae**. Discoidal and involute shells with well-defined and often profusely tuberculated costations which are interrupted on the ventral aspect by a smooth zone or channel. This may in some specialised forms become a distinct channel bordered

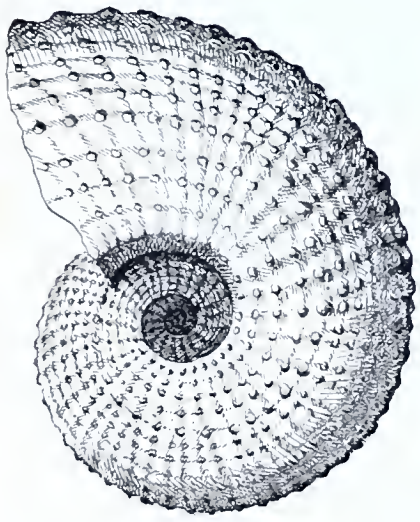


Fig. 1147.

Trachyceras Austriacum, Mojs. Upper Trias; Röthelstein, near Aussee, Austria.

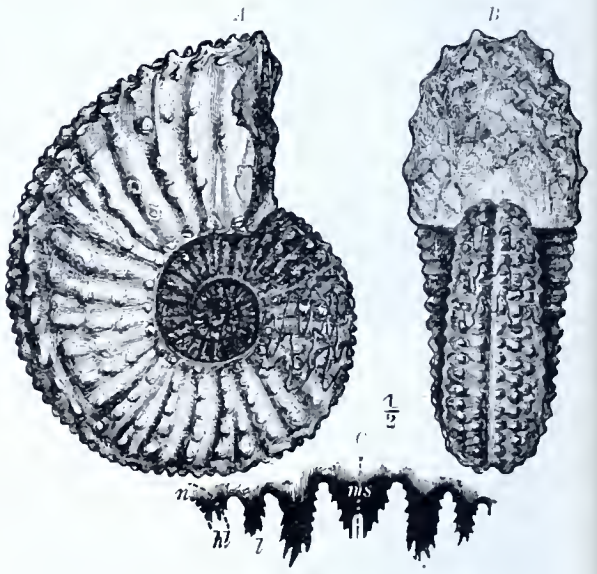


Fig. 1148.

Protrachyceras Archelaus, Laube. Upper Trias (Norian); Bakony, Hungary (after Mojsisovics).

by tuberculated ridges. Lobes and saddles completely divided by marginals, but these do not become very long nor complex.

Distichites, *Trachyceras* (Fig. 1147), *Protrachyceras* (Fig. 1148), *Anolcites*, *Sandlingites*, *Sirenites*, *Anasirenites*, *Diplosirenites*, Mojs. Trias. (?) *Hesperites*, Pompeckj. Rhaetic.

Family 17. **Tibetitidae**. Compressed involute forms with channeled venter as in *Arpaditidae*, but sutures generally with adventitious inflections developed through division of the first pair of primitive lateral saddles. Auxiliary series developed by division of the large internal saddles.

Anatibetites, *Tibetites*, *Paratibetites*, *Hauerites*, Mojs. Trias.

Family 18. **Pinacoceratidae**. Mojsisovics. Compressed, more or less involute forms with rounded venter only in primitive species. Sutures greatly complicated, convex, and with adventitious inflections; also often with a corresponding series of

auxiliaries. Ventral lobe in some forms similar to that in *Tirolitidae*, and mode of generation of adventitious inflections in *Placites* is the same as in *Tibetitidae;* that in *Pinacoceras* is unknown.

Placites, *Bambaganites*, *Pinacoceras* (Figs. 1149, 1150), Mojs. Trias.

Family 19. **Choristoceratidae**. Discoidal ammoniticones in primitive forms, becoming uncoiled phylogerons, and finally even complete baculiticones in the most specialised species. Sutures also phylogerontic, having only six entire or very faintly denticulated lobes, and six entire saddles. Ventral lobe divided, and the antisiphonal either entire or bifid at its extremity. Dorsal lobes and saddles otherwise entire. Connected through *Polycyclus* with *Buchites*, according to Mojsisovics.

Polycyclus (Fig. 1151), *Peripleurites*, Mojs.; *Choristoceras* (Fig. 1152), *Rhabdoceras* (Fig. 1153), Hauer. Trias.

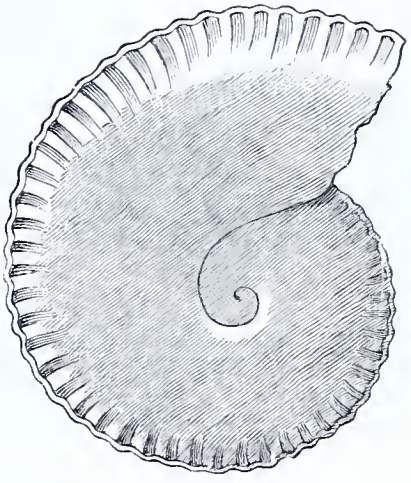


FIG. 1149.

Pinacoceras Layeri, Hauer sp. Upper Trias; Rothelstein, near Aussee, Austria.

Family 20. **Cochloceratidae**. Turriliticones with costae similar to those of preceding family, but more or less asymmetrical

FIG. 1150.

Pinacoceras Metternichi, Hauer sp. Keuper; Someraukogel, near Hallstadt, Austria. Suture-line reduced (after Hauer).

in consequence of the asymmetry of the spires. Lobes reduced to four in number,

FIG. 1151.

Polycyclus nasturtium, Dittmar sp. Keuper; Sandling, near Aussee.

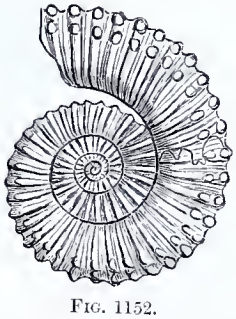


FIG. 1152.

Choristoceras Marshi, Hauer. Rhaetie; Kendelengraben am Osterhorn, near Salzburg.

FIG. 1153.

Rhabdoceras Suessi, Hauer. Keuper; Sandling, near Aussee (after Hauer).

FIG. 1154.

Cochloceras Fisheri, Hauer. Sandling, near Aussee (after Hauer).

and there are other phylogerontic suppressions. Funnels monochoanitic, collars absent.

Cochloceras, Hauer (Fig. 1154); *Paracochloceras*, Mojs. Trias.

Sub-Order G. PHYLLOCAMPYLI. Hyatt.

An extensive series of genera having saddles with rounded outlines in primitive forms, and as a rule with phylloidal bases in sutures with divided lobes. When the saddles are completely divided by marginal lobes, the marginal saddles still retain the same monophyllic outline. Dorsal lobes and saddles generally numerous, except in primitive forms. Antisiphonal lobe entire only in primitive forms, becoming bifid with more or less persistently entire sides in some groups even in the Jura and Cretaceous, but in others they may become either bifid or trifid, and in highly specialised Triassic forms may acquire considerable complexity of outline. The zygous dorsal saddles are commonly monophyllic.

I. Prolecanitida.

The young in this group have an ibergiceran stage (Karpinsky) with very long undivided ventral lobe. Primitive forms are compressed, discoidal, and more specialised genera become involute and assume a modified anarcestean aspect. Saddles are entire in the former, but the first laterals become very large and are subdivided by simple marginal lobes. Lateral lobes entire in primitive genera, and become bifid or trifid in specialised forms, but rarely have more numerous digitations. Antisiphonal lobe entire or pointed. Siphuncle without calcareous sheath; funnels monochoanitic so far as known.

Fig. 1155.

Prolecanites lunulicosta, Sandb. Upper Devonian; Nassau (after Sandberger).

Family 1. **Prolecanitidae.** Shells discoidal or involute, compressed, subquadrate, or helmet-shaped in section, but never semilunate except during the anarcestean stage of the young. Primitive forms have undivided ventral lobes, and rounded saddles and lobes of the lecanitean type; sometimes also they have large inner saddles showing derivation from *Magnosellaridae*, but there are not less than two lateral lobes. More specialised shells have entire hastate lobes and saddles, and similar but divided ventral lobes. Aperture with well-marked hyponomic sinus. Shells smooth or costated, and often with longitudinal ridges.

Ibergiceras, Karp.; *Prolecanites*, Mojs. (Fig. 1155); *Agathiceras*, *Doryceras*, *Adrianites*, *Clinolobus*, Gemm. Devonian to Permian.

Fig. 1156.

Pronorites cyclolobus, Phill. sp. Carboniferous Limestone; Grassington, Yorkshire (after Phillips).

Family 2. **Noritidae.** Waagen. Similar to *Prolecanitidae*, but the ventral lobe instead of becoming divided in the usual way, retains the larval trifid stage throughout life in primitive species. In specialised forms the larval siphonal saddles enlarge in the neanic stage, thus building up a single siphonal saddle with a comparatively large siphonal lobe. First lateral lobes may be bifid, trifid, or completely digitated in specialised shells, and when the second and other lateral lobes also become digitated the outlines are ceratitic. The saddles, however, retain more or less of their primitive outlines, and their bases are entire. Sutures without true adventitious inflections. Apertures have crests at the ventro-lateral angles; straight or with faint sutures at the venter, but replaced by slight crests in some Triassic genera.

Fig. 1157.

Suture-line of *Norites Gondola*, Mojs. Muschelkalk; Schreyer-Alp, near Hallstadt, Austria.

Paraproleeanites, Karp.; *Pronorites*, Mojs. (Fig. 1156); *Parapronorites*, *Daraelites*, Gemm.; *Ambites*, Waagen; *Norites*, Mojs. (Fig. 1157).

Family 3. **Medlicottidae.** Shells compressed, discoidal, and involute, with smooth or costated sides, and often costated or tuberculated and channeled venter. Ventral lobe entire in primitive species, and trifid or divided as in primitive *Pronoritidae* in more specialised forms. First lateral saddles simple but divided in primitive genera, and acquire in *Medlicottia* through hypertrophy and the development of marginals extraordinary serrated outlines. Aperture as in *Pronoritidae*.

Fig. 1159.

Suture-line of *Medlicottia primas*, Waagen. Permo-Carboniferous; Salt Range, India (after Waagen).

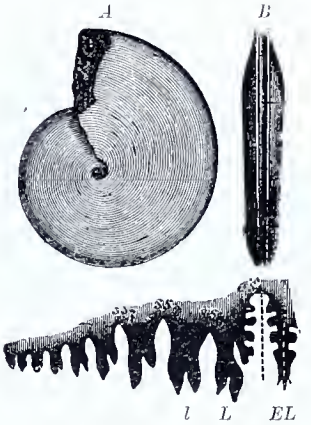


Fig. 1158.

Medlicottia Trautscholdi, Gemm. Permo-Carboniferous; Sosio, Sicily (after Gemmellaro).

Sieanites, Gemm.; *Promedlicottia*, Karp.; *Propinaeoceras*, Gemm.; *Medlicottia*, Waagen (Figs. 1158, 1159). Permian.

II. Lobitida.

An isolated group resembling Anarcestidae through the phylogerontic contraction of the living chamber, but sutures similar to those of Prolecanitidae. Saddles entire, but the lateral lobes are bifid in the young, and the median marginals in these lobes, becoming larger by growth, are often nearly equal in size to the more primitive laterals in ephebic stages. Antisiphonal lobe bifid and other dorsal inflections entire and similar to those of Prolecanitidae.

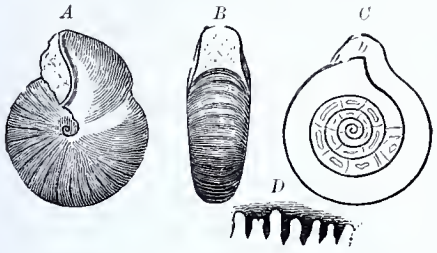


Fig. 1160.

Lobites delphinocephalus, Hauer sp. Upper Trias; Sandling, near Aussee, Austria. *A*, *B*, External aspect. *C*, Median section. *D*, Suture-line, 1/1.

Family 4. **Lobitidae.** Only two primitive lateral lobes are developed in early neanic sub-stages; the others arise by hypertrophy of the secondary marginal saddles, which subsequently divide the primitive lobes. Antisiphonal lobe bifid. Aperture in ephebic stage normal and with slight ventral crests; contracted and more or less distorted in gerontic stage.

Fig. 1161.

Lobites pisum, Münst. sp. Keuper (Carniolan); St. Cassian, Tyrol.

Includes only *Lobites*, Mojs. (Figs. 1160, 1161), from the Alpine Trias.

III. Arcestida.

Conchs more or less smooth, involute, rarely discoidal, invariably Anareestes-like, similar to many of the preceding groups, but with more complex sutures. Finally in Areestidae and Cladiseitidae the proleeanitean outline survives as a rule only in the peculiar straightness and uniform size of the lobes and saddles. The retention of monophyllie outlines in the inner saddles and in the dorsal sutures, as well as in the young stages, occurs in some forms, however, even in these families.

Family 5. **Popanoceratidae.** Shells similar to *Arcestidae* (except in primitive *Popanoceras*, which is discoidal and compressed). Saddles have entire monophyllic bases, and dorsal sutures are similar to those of *Prolecanitidae* in some genera; but in

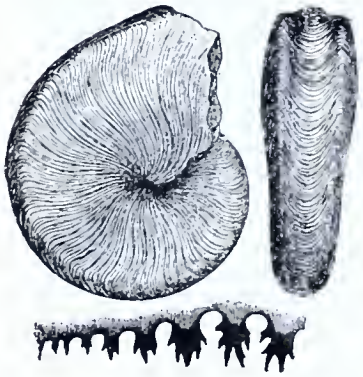


Fig. 1162.

Popanoceras multistriatum, Gemm. Permo-Carboniferous; Sosio, Sicily. $^2/_3$ (after Gemmellaro).

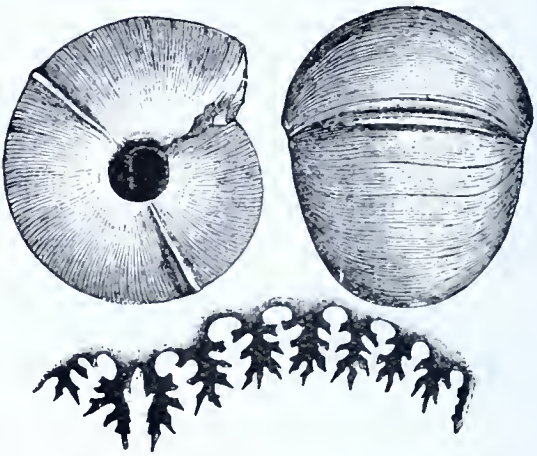


Fig. 1163.

Cyclolobus Stachei, Gemm. Permo-Carboniferous; Sosio Sicily (after Gemmellaro).

others they become more complex and show approximation to *Arcestidae*. Antisiphonal lobe trifid, but otherwise entire in primitive forms, becoming complex in specialised

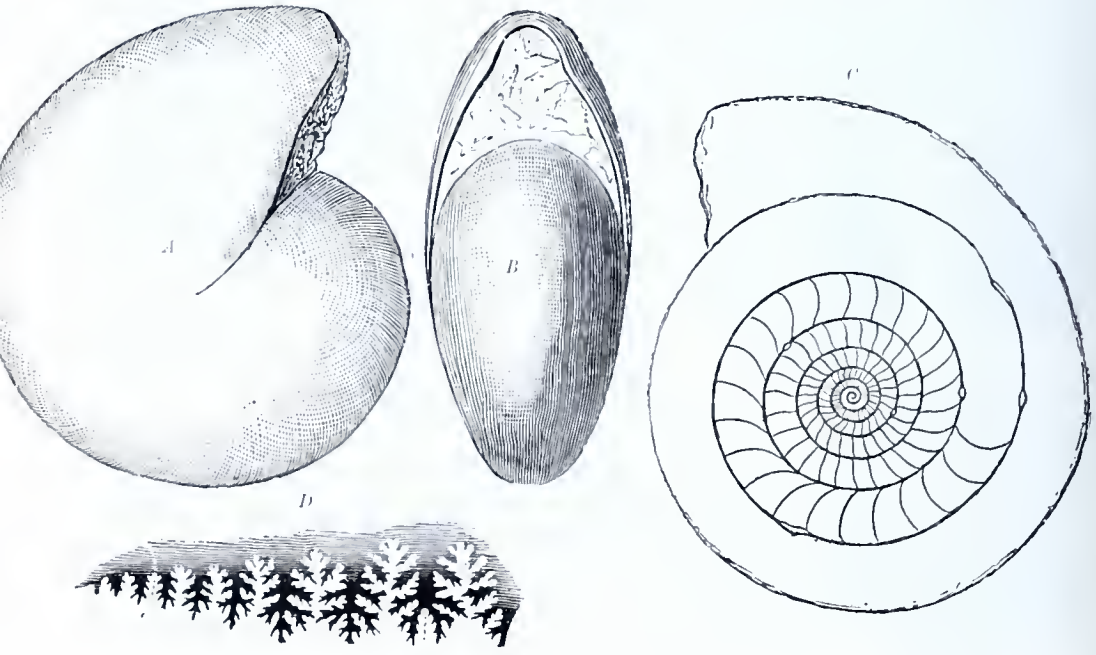


Fig. 1164.

Arcestes intuslabiatus, Mojs. Upper Trias; Steinbergkogel, near Hallstadt, Austria. *A*, *B*, External aspect. *C*, Median section. *D*, Suture-line.

genera. Aperture with hyponomic sinus in primitive genera, but acquires faint crests in shells that resemble Arcestidae.

Stacheoceras, *Waagenoceras*, *Hyattoceras*, Gemm.; *Popanoceras*, Hyatt (Fig. 1162); *Parapopanoceras*, Haug; *Cyclolobus*, Waagen (Fig. 1163). Permian and Trias.

Family 6. **Arcestidae.** Mojsisovics (*pars*). Smooth, globose, deeply involute

anarcestean forms, discoidal only in primitive genera. Gerontic living chamber usually more or less contracted laterally, becoming sometimes subacute at the venter; in extreme age depressed, and truncated or concave at the aperture. The latter has normally in the ephebic stage a low broad ventral crest, but loses this in the parageruntic sub-stage, and acquires a ventral sinus simulating that of Palaeozoic and more primitive forms. Saddles and lobes completely divided by more or less complex marginals, the monophyllic outline being completely obscured except in the young, and in dorsal sutures of some species. Siphonal saddles long, and not very deeply incised by marginal lobes. Antisiphonal lobe bifid or trifid, and complex in specialised forms. Other dorsals may also become quite complex, and as a rule are completely divided, although of course simpler than the external sutures. Dorsal sutures in the young resemble those of *Popanoceratidae*. Funnels chloiochoanitic in ephebic stage.

Fig. 1166.

Suture-line of *Didymites subglobus*, Mojs. Upper Trias; Someraukogel, near Hallstadt (after Mojsisovics).

Fig. 1165.

Joannites cymbiformis, Wulfen. Upper Trias; Raschberg, near Aussee, Austria. Natural cast showing living chamber (after Mojsisovics).

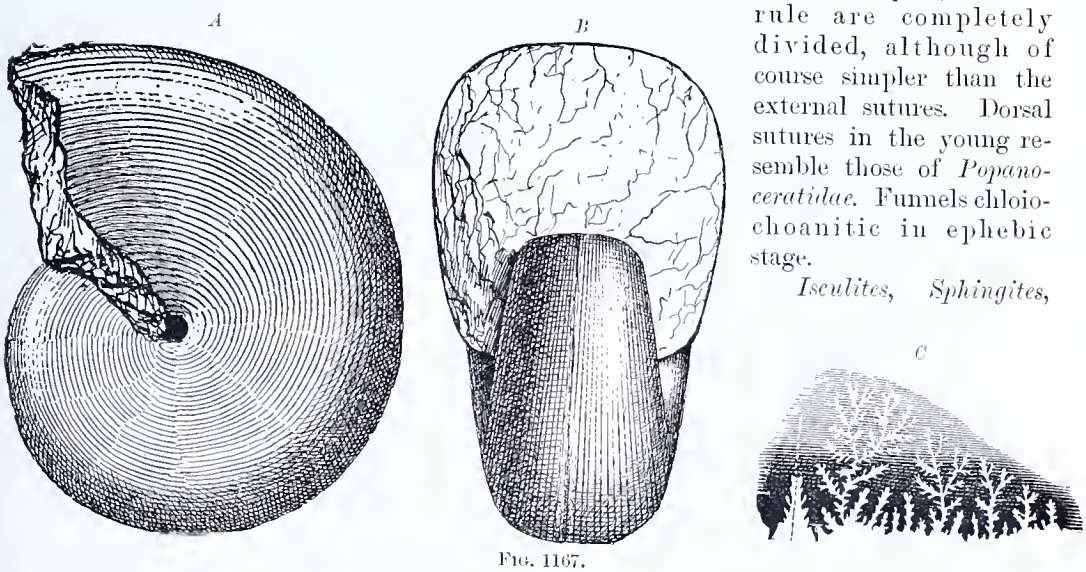


Fig. 1167.

Cladiscites tornatus, Bronn sp. Upper Trias; Steinbergkogel, near Hallstadt, Austria. *A*, *B*, Side and front views. *C*, Suture-line.

Isculites, *Sphingites*, *Arcestes* (Fig. 1164), *Stenarcestes*, *Proarcestes*, *Pararcestes*, *Ptycharcestes*, *Joannites*, Mojs. (Fig. 1165); *Rhaetites*, gen. nov. Type *R.* (*Arc.*) *rhaeticus*, Clark sp. Trias.

Family 7. **Didymitidae**. Mojsisovics. Conchs globose like *Arcestidae*, but having growth-lines evenly concave on the sides instead of sigmoidal, and sutures with

solid broad bifid saddles. The division of these by large secondary lobes is similar to that which occurs in the first laterals of *Mantiiceras* and *Sporadoceras*, but affects more of the primitive laterals. Aperture with only short broad crests on the venter.

Includes only *Didymites*, Mojs. (Fig. 1166), from the Alpine Trias.

Family 8. **Cladiscitidae**. Zittel. Some shells resembling *Arcestidae*, but typically the sides are flat, venter plano-convex, and surface usually covered with longitudinal ridges. Sutures similar to *Arcestidae*, but more complex, the saddles being reduced in many forms to thread-like narrowness. Growth-lines like those of *Didymites* on the sides, but have crests at the ventro-lateral angles, and very broad ventral crests.

Cladiscites (*Hypocladiscites*), (Fig. 1167); *Psilocladiscites*, *Procladiscites*, *Paracladiscites*, Mojs. Trias.

IV. Phylloceratida.

Shells as a rule with peculiar, prominent bands of growth. Saddles in primitive genera have the monophyllic bases of those in Popanoceratidae, but in more specialised groups the marginal saddles alone retain the same rounded outlines. Dorsal saddles and lobes are, as a rule, at least three in number. Antisiphonal lobe often bifid and retains either entire outlines on both sides, or with a few simple marginals, or has but one pair of short lateral branches. Aperture with well-marked but short ventral crest.

Family 9. **Megaphyllitidae**. Mojsisovics. Conchs compressed, discoidal, or involute. Sutures with primitive monophyllic saddles, and more regular in the relative size of the lobes and saddles and in their marginals than succeeding families. Antisiphonal lobe bifid but otherwise entire.

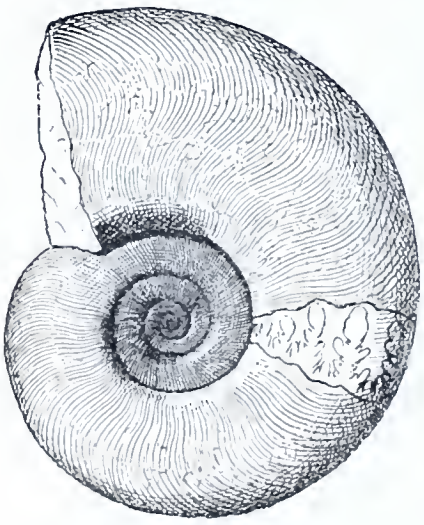


Fig. 1165.

Monophyllites Simonyi, Hauer sp. Upper Trias; Rothelstein, near Aussee, Austria.

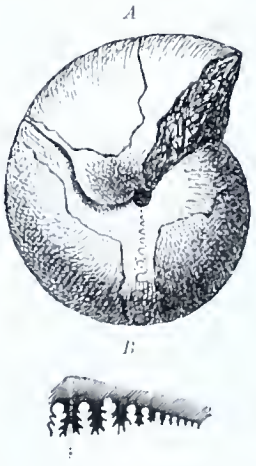


Fig. 1169.

A, *Megaphyllites insectus*, Mojs. Upper Trias; Sandling, near Aussee, Austria. *B*, Suture-line of *M. Jarbas*, Munst.

Monophyllites (Fig. 1168), *Megaphyllites*, Mojs. (Fig. 1169); *Mojsvarites*, Pompeckj; *Discophyllites*, gen. nov. Type *D.* (*Lytoc.*) *patens*, Mojs. sp. Trias.

Family 10. **Ussuritidae**. Conchs compressed, discoidal, and involute. Sutures have modified monophyllic first lateral saddles, the second laterals more or less pointed in *Ussuria*. Auxiliary series remarkably irregular, and all the lateral lobes with very large, more or less pointed, but still phylloidal marginal lobes and saddles. Ventral lobe broad and short, and siphonal saddle very large.

Ussuria, Diener; *Ussurites*, gen. nov. Type *U.* (*Monophyl.*) *sichotieus*, Diener sp. Trias.

Family 11. **Phylloceratidae**. Zittel. Principally involute shells with very complex sutures, which, however, still retain monophyllic outlines in the marginal saddles. Antisiphonal lobe with entire sides, or with only one pair of short lateral branches, and extremities usually bifid.

Rhacophyllites, Zittel (Fig. 1170); *Euphyllites*, Wähner; *Phylloceras*, Suess (Figs.

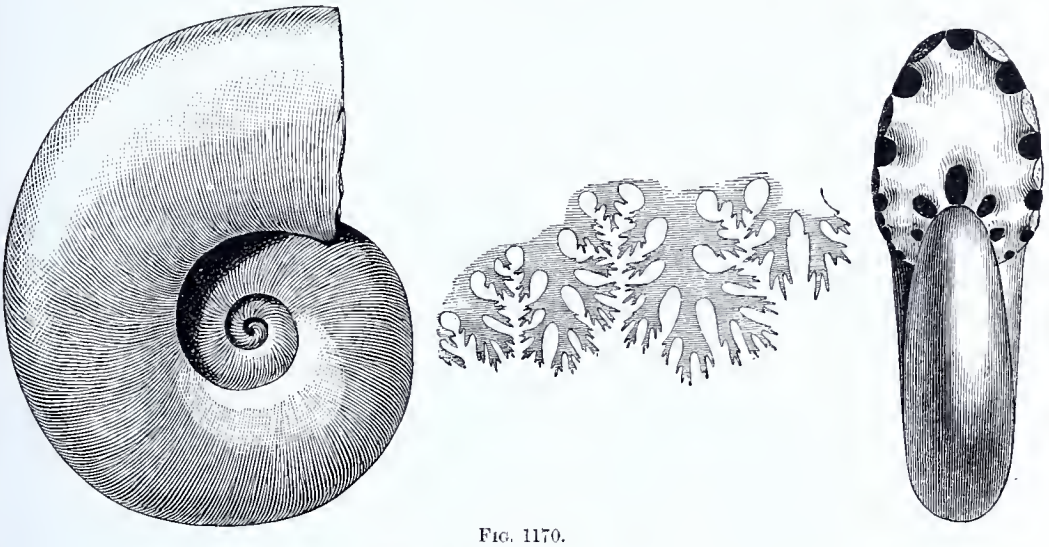


Fig. 1170.

Rhacophyllites neojurensis, Quenst. sp. Keuper; Hallstadt, Austria.

Fig. 1171.

Phylloceras heterophyllum, Sowb. sp. Upper Lias; Whitby, Yorkshire.

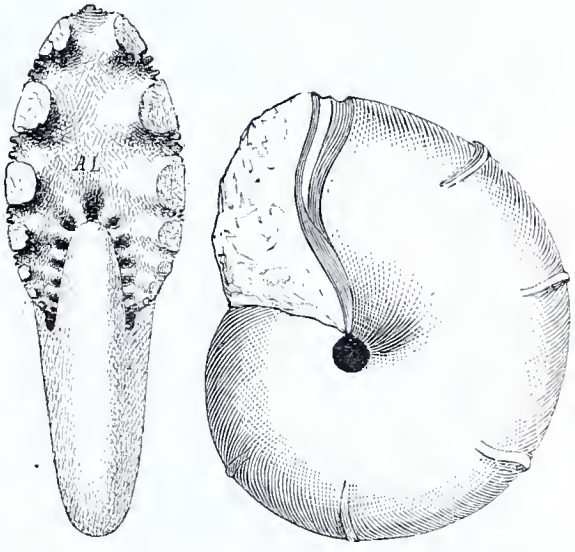


Fig. 1172.

Phylloceras ptychoicum, Quenst. sp. Tithonian; Stramberg, Moravia. *AL*, Antisiphonal lobe.

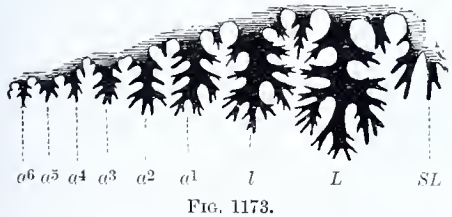


Fig. 1173.

Suture-line of *Phylloceras Nilssoni*, Heb. sp. Upper Lias.

Fig. 1174.

Suture-line of *Sowerbiceras tortisulcatus*, d'Orb. sp. (after Quenstedt).

SL, Ventral or siphonal lobe; *L*, First, and *l*, Second lateral lobes; a^{1-6}, Inner or so-called auxiliary lobes; *n*, Line of involution; *Li*, Second dorsal lobe; *AL*, Antisiphonal lobe.

1171-1173); *Sowerbiceras*, Paroni and Bon. (Fig. 1174); *Dasyceras*, gen. nov. Type

D. (*Phyl.*) *rakosense*, Herbich sp.; *Schistophylloceras*, gen. nov. Type *S.* (*Phyl.*) *aulonotum*, Herbich sp.; *Geyeroceras*, gen. nov. Type *G.* (*Phyll.*) *cylindricum*, Geyer sp.; *Tragophylloceras*, gen. nov. Type *T.* (*Phyl.*) *heterophyllus-numismalis*, Quenst. sp.; *Meneghiniceras*, gen. nov. Type *M.* (*Phyl.*) *lariense*, Menegh. sp. Trias to Cretaceous.

Sub-Order H. LEPTOCAMPYLI. Hyatt.

Shells with peculiar, more or less crenulated ornamentation, due to the intersection of two systems of lines, transverse bands of growth, and longitudinal creases and ridges, sometimes developing into spines. Aspect more discoidal and larval, and with fewer highly involute forms than in other sub-orders. Shell often constricted as in Phyllocampyli. Characterised in some families by the small number of completely developed lobes and saddles. Outlines of sutures extremely complex, and saddles generally much reduced owing to excessive development of the lobes.

The antisiphonal lobe has in most families a cruciform aspect, due to the development of a large pair of branching marginal lobes. In the *Lytoceratidae* there is also an inward growth of the two marginals near the tips, so that they rest upon the oral surfaces of the septa instead of against the inner surface of the dorsum; these modifications being peculiar to this sub-order. The principal inflections are more numerous in the young, and reduction takes place in later stages through arrested development and suppression of those nearest the lines of involution. Wähner's thorough researches have shown the close affinities of *Pleuracanthites* with *Psiloceras* and *Caloceras*, which lie at the ancestral base of this sub-order. This accounts for the similarities between the young of this group and *Phylloceratidae*, as demonstrated by J. P. Smith. A number of phylogerontic uncoiled genera occur in the Cretaceous.

Family 1. **Pleuracanthitidae.** Discoidal, plicated, or costated shells, having crescentic tubercles or hollow spines in some species; venter rounded except in extreme age of a few species, in which a faint keel appears. Aperture has a short rostrum with deep ventro-lateral or lateral sinuses, and lateral or dorso-lateral crests.

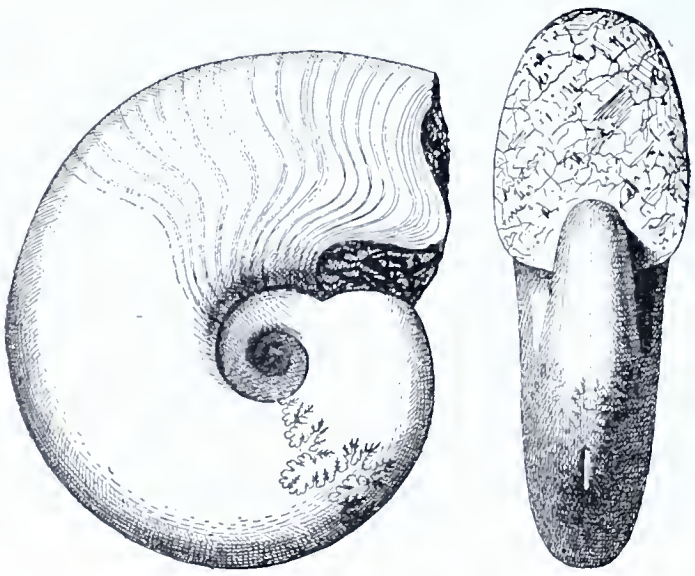


Fig. 1175.

Haploceras elimatum, Oppel sp. Tithonian; Stramberg, Moravia.

Pleuracanthites, Canavari; *Analytoceras*, gen. nov. Type *A.* (*Lyt.*) *articulatum*, Wähner sp. Lias.

Family 2. **Tetragonitidae.** Smooth, discoidal, and involute shells, with flattened or rounded venter, and more or less flattened sides. Constrictions and spines sometimes present. Sutures sometimes reduced to four paired saddles and three lobes on the dorsum, or there may be only two pairs, or a single pair of large saddles. Siphonal lobes deeper and broader than in *Lytoceratidae*, the siphonal saddles larger, and laterals more numerous, comprising sometimes as many as nine pairs of complex zygous lobes and saddles. Antisiphonal lobe straight, complex, trifid, or bifid.

Tetragonites, *Pseudophyllites*, Kossmat; *Gaudryceras*, Grossouvre; *Protetragonites*, gen. nov. Type *P.* (*Amm.*) *quadrisulcatus*, d'Orb. sp. Cretaceous.

Family 3. **Haploceratidae.** Zittel. Mostly involute shells, smooth, or with constrictions and fold-like costae without tubercles that commonly follow the lines of growth across the rounded venter uninterruptedly. Spines sometimes present as in preceding family. Sutures have blunt siphonal saddles, never pointed. First lateral lobes shallower than in *Lytoceratidae*, the first lateral saddles broader, and less deeply cut by marginals. Antisiphonal lobe long, straight, and trifid. Lateral zygous inflections more numerous, and there are often three or more zygous dorsal saddles.

Haploceras, Zittel (*Lissoceras*, Bayle), (Fig. 1175). Jura and Cretaceous. *Eurynoticeras*, Canavari. Jura. *Desmoceras*, Zittel (Figs. 1176, 1177); *Puzosia*, Bayle; *Cleonoceras*, Paroni and Bon.; *Schlueteria*, *Hauericeras*, Grossouvre. Cretaceous.

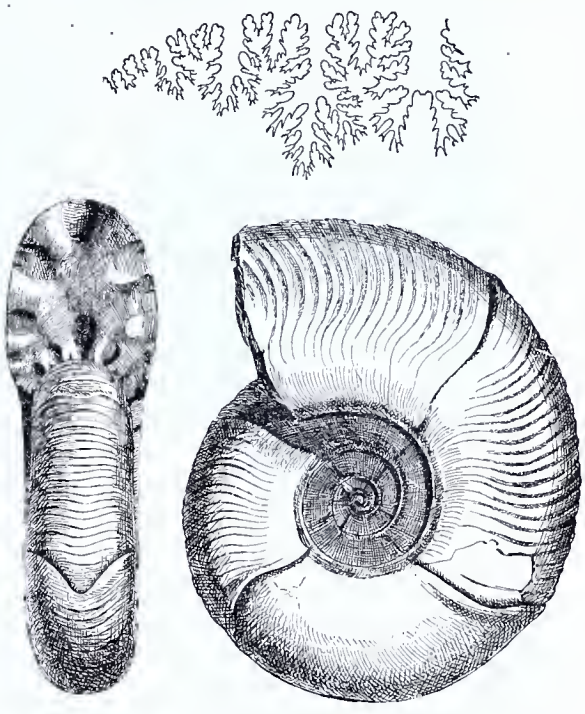


Fig. 1176.

Desmoceras Mayorianum, d'Orb. sp. Gault; Perte du Rhône (after d'Orbigny).

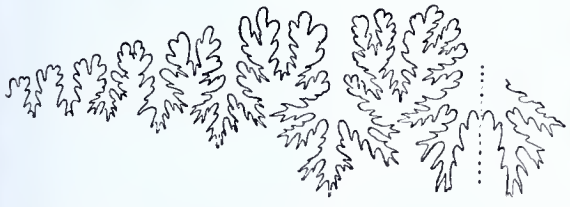


Fig. 1177.

Suture-line of *Desmoceras latidorsatum*, Mich. Gault; Perte du Rhône.

Fig. 1178.

Creniceras Renggeri, Oppel. sp. Oxfordian; Salins, Jura.

Family 4. **Glochiceratidae.** Discoidal and involute shells, smooth in primitive species, but acquiring highly inflected costations, sometimes with two rows of tubercles on the sides, and a median ventral row that may fuse into a continuous solid keel. One line of ventral tubercles may also arise directly from folds that appear in otherwise unornamented shells. Aperture sometimes with long lateral lappets similar to those of *Oppelidae*. Sutures similar to *Haploceratidae*.

Cadomoceras, *Creniceras*, Mun.-Chalm. (Fig. 1178); *Cyrtosiceras*, gen. nov. (Fig. 1179). Type *C.* (*Amm.*) *macrotelus*, Oppel sp.; *Glochiceras*, gen. nov. (Fig. 1106). Type *G.* (*Amm.*) *nimbatum*, Opp. sp.; *Phlycticeras* (*Lophoceras*, Bonar.), *Ochetoceras*, Haug (Fig. 1180); *Cymaceras*, Quenst. (Hyatt). Type *C.* (*Amm.*) *Guembeli*, Opp. sp. *Strigoceras*, Quenst. (Buckman); *Streblites*, gen. nov. (Fig. 1181). Type *S.* (*Amm.*) *pictus-costatus*, Quenst. sp. Middle and Upper Jura.

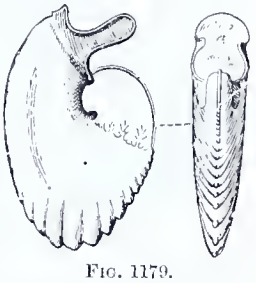


Fig. 1179.

Cyrtosiceras macrotelus, Oppel sp. Tithonian; Stramberg, Moravia.

Family 5. **Distichioceratidae**. Sutures simpler than in *Glochiceratidae*, owing

Fig. 1180.

Oehetoceras flexuosum, v. Buch sp. Upper Jura (3); Laufen, Würtemberg.

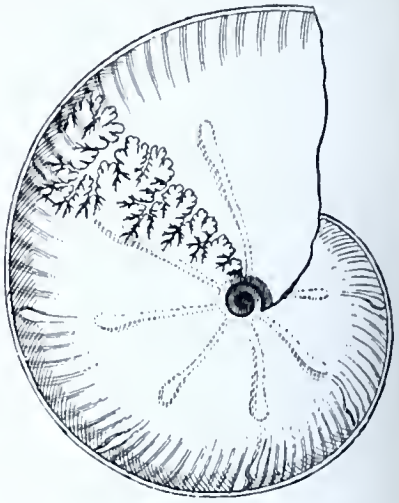
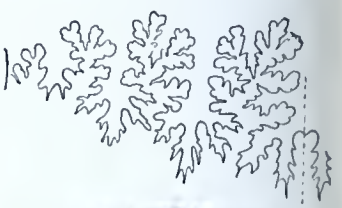


Fig. 1181.

Streblites tenuilobatus, Oppel sp. Upper Jura; Pappenheim, Bavaria.

to arrested development. Young of *Distichioceras* repeat the characteristic form and costae of the latter, with smooth venter and lateral tubercles, and then acquire the features of *Horioceras* before the median continuous keel of *Distichioceras* arises.

Includes *Horioceras* and *Distichioceras*, Munier-Chalmas. Jura.



Family 6. **Silesitidae**. Similar to *Haploceratidae*, but costae more strongly developed, and sometimes spinous.

Silesites, *Holcodiscus*, Uhlig; *Pachydiscus*, Zittel (Figs. 1182, 1183); *Parapachydiscus*, gen. nov. Type *P.* (*Amm.*) *gollevillensis*, d'Orb. sp.; *Pseudohaploceras*,

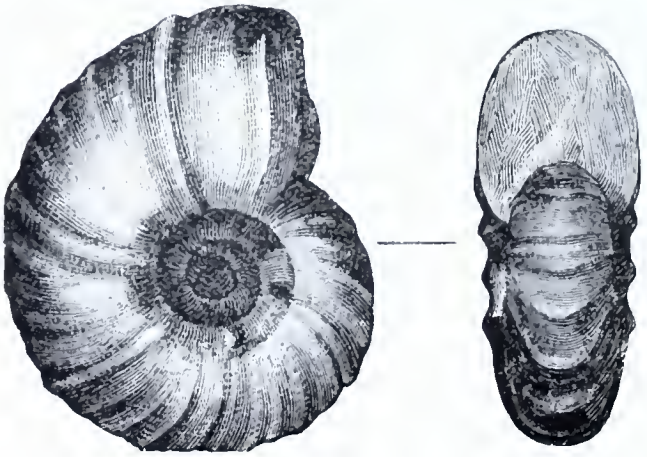


Fig. 1182.

Pachydiscus peramplus, Mantell sp. Lower Chalk; England.

Fig. 1183.

Pachydiscus Wittekindi, Schlüter sp. Upper Cretaceous; Haldem, Westphalia. 1/3.

gen. nov. Type *P.* (*Hapl.*) *liptoviense*, Uhlig sp.; *Gabbioceras*, gen. nov. Type *G.*

(*Amm.*) *Batesi*, Gabb sp. (*Palaeont. California*, II., Pls. 20, 21; non *A. Batesi*, I., Pl. 13); *Pleuropachydiscus*, gen. nov. Type *P.* (*Amm.*) *Hoffmani*, Gabb sp. Cretaceous.

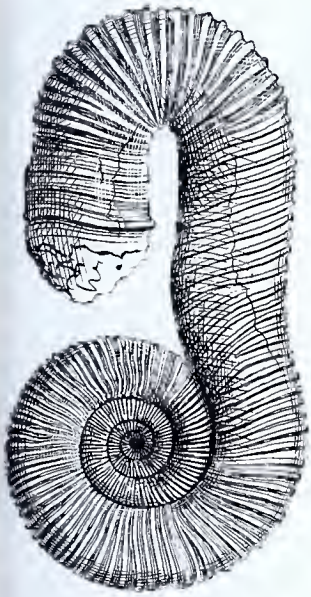


Fig. 1184.

Macroscaphites Ivanii, d'Orb. sp. Upper Neocomian; Mallenewitz, Carpathia.

Fig. 1185.

Ptychoceras Puzosianum, d'Orb. sp. Barremian; Vergons, Basses Alpes.

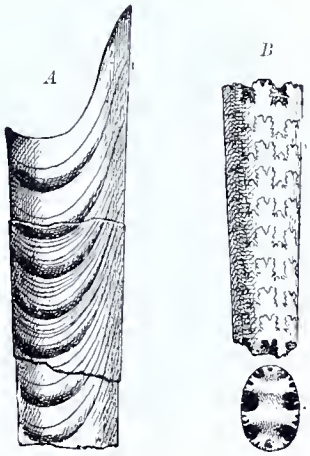


Fig. 1186.

A, *Baculites anceps*, Lam. *B*, *B. Faujasi*, Lam. Upper Cretaceous; Maestricht.

Fig. 1187.

Suture-line of *Diplomoceras cylindraceum*, Defr. Uppermost Cretaceous; Tresville, Manche.

Family 7. **Macroscaphitidae**. Symmetrical, closely coiled, discoidal ammoniticones during young stages (and persistently so in primitive forms), but becoming uncoiled in gerontic stages or earlier in the ontogeny of phylogerontic forms, and finally straight in some genera. Antisiphonal lobe short, and in some genera trifid. Shells have constrictions and large costae at intervals, but no tubercles at any stage.

Macroscaphites, Meek (Fig. 1184); *Leptoceras*, *Costidiscus*, Uhlig; *Tropaeum*, Sowb.; *Ptychoceras*, d'Orb. (Fig. 1185); *Diptychoceras*, Gabb; *Cyrtochilus*, Meek (*Scipionoceras*, Hyatt); *Baculites*, Lam. (Fig. 1186); *Diplomoceras*, gen. nov. (Fig. 1187). Type *D.* (*Ham.*) *cylindraceum*, d'Orb. sp.; *Anahamulina*, gen. nov. (Fig. 1188, *A*). Type *A.* (*Ham.*) *subcylindrica*, d'Orb. sp. Cretaceous.

Family 8. **Scaphitidae**. Meek. Two or more rows of tubercles developed in the ephebic or gerontic stage; costae continuous across the venter; aperture evenly constricted on the sides and with a slight, broad rostrum on the venter, caused by recession of the lateral curves. There is a dorsal lappet, but this is long and bent only in *Jahnnites*. The young and sometimes ephebic stages of *Scaphites* possess the costae, form, and general aspect of *Pachydiscus*, and there are species transitional between them.

Fig. 1188.

A, *Anahamulina subcylindrica*, d'Orb. sp. *B*, Suture-line of *A. Lorioli*, Uhlig sp. Neocomian; Anglès, Basses Alpes (after Uhlig).

Scaphites, Park. (Figs. 1189, 1190); *Discoscaphites*, Meek; *Anascaphites*, gen. nov. Type *A.* (*Scaph.*) *ventricosus*, Meek sp.; *Jahnites*, gen. nov. Type *J.* (*Scaph.*) *Geinitzi*, var. *binodosus*, Jahn. sp. Cretaceous.

Fig. 1189.

Scaphites spiniger, Schluter. Upper Cretaceous (Senonian); Coesfeld, Westphalia.

Fig. 1190.

Scaphites aequalis, Sowb. Cenomanian; Rouen, France. 1/1.

Family 9. **Lytoceratidae**. Neumayr (*pars*).

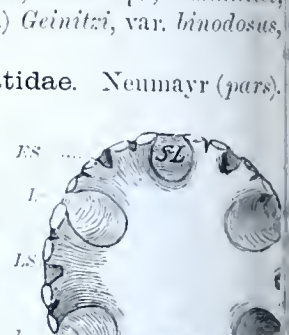


Fig. 1191.

Lytoceras fimbriatum, Sowb. sp. Middle Lias; Würtemberg. Cross-section (cf. Fig. 1099).

Includes only closely coiled, discoidal, and involute shells with somewhat prominent, often crenulated transverse bands of growth. Antisiphonal lobe with two long internal branches bending inwards and attached to surfaces of the septa. Siphonal lobe short like that of *Phylloceras*, and siphonal saddles narrow. The first lateral saddles small and short, the first lateral lobes much longer than the ventral. Reduction of lobes along the line of involution is such that there are commonly only six to eight in full-grown shells.

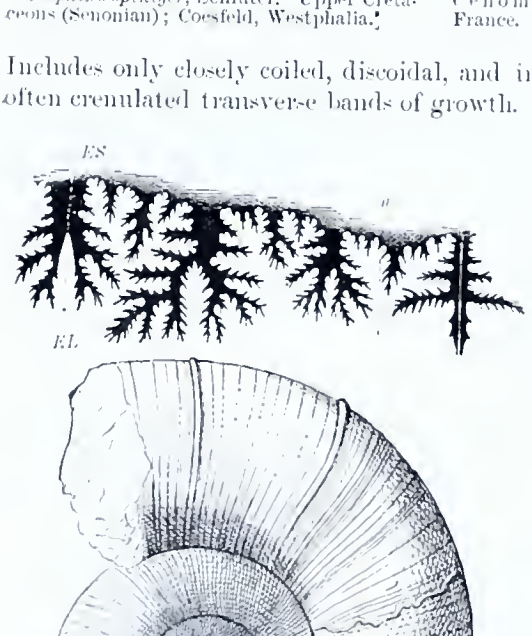


Fig. 1192.

Lytoceras Liebigi, Oppel sp. Tithonian; Stramberg, Moravia.

Lytoceras, Suess. (*Thysanoceras*,

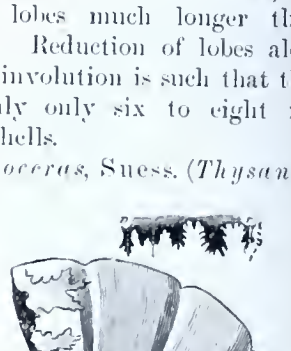


Fig. 1193.

Alocolytoceras Germaini, d'Orb. sp. Upper Lias; Pinperdu, near Salins, Jura.

Hyatt), (Figs. 1191, 1192). Jura and Cretaceous. *Alocolytoceras*, gen. nov. (Fig. 1193). Type *A.* (*Amm.*) *Germainei*, d'Orb. sp.; *Pleurolytoceras*, gen. nov. Type *P.* (*Amm.*) *hircinum*, Schloth. sp. Jura.

Incerta sedis. *Ectocentrites*, Wähner. Venter crossed by costae that become oncave or flattened, and bordered by two rows of tubercles in the young; in later ages the venter is rounded and crossed by costae without tubercles. Sutures similar o those of this sub-order. Antisiphonal lobe straight, bifid; the first pair of dorsal ddles are so large that the extremities are external to lines of involution.

Sub-Order I. PACHYCAMPYLI. Hyatt.

Shells attaining the acme of complexity in evolution of costae ornamented with spines, nd often combined in the same forms with keeled and channeled venters. Sutures, how-ver, are not correspondingly developed, and as regards both number and outlines of their obes and saddles are less complex than in Phyllocampyli. Lobes and saddles as a rule orter, broader, and less arborescent than in either Leptocampyli or Phyllocampyli. haracteristic type of sutural outline "Arietean" or unequal. First pair of lateral ddles generally broad, solid-bodied, and bifid; first pair of lobes adjoining these usually uch longer and larger than any others.[1] *Second pair of lobes and saddles do not velop in similar proportions to the first pair, and consequently often appear to belong to e later developed auxiliaries. Ventral lobe usually deep, and has a trifid or bifid phonal saddle, which is usually digitated throughout, and never has the elongated, iangular, and often smooth outline of that in preceding sub-orders.*

The ventral lobe becomes stouter and broader in proportion, and simpler in outline as a le in normal Cretaceous forms, and these generally have less complex sutures than Jurassic ells. Finally, in the phylogerontic *Tissotidae*, *Placenticeratidae*, etc., the ventral lobe comes much broader and shorter, and the siphonal saddle is proportionally affected. The rsal series of inflections are almost as limited in the primitive Lower Liassic forms as in *ptocampyli*, consisting only of one very long antisiphonal lobe, a pair of long first lateral ddles, and a pair of zygous lobes often incomplete on the outer sides. Where the dorsum is oader and more involute, however, there may be two, three, or more pairs of zygous dorsal ddles and an equal number of lobes. These are almost invariably complex in outline, and e antisiphonal may be bifid or trifid.

Phylogerontic forms occur sporadically in the Jura and generally throughout the Creta-ous. They are of two kinds: (1) Those that are retrogressive as compared with their cestors in complexity of sutures only. Sometimes, as in *Spheniscidae* and *Engonoceratidae*, ey are highly involute shells; or, as in *Tissotia*, etc., they may be more discoidal and dose. (2) Those that are retrogressive as regards both form and sutures, like *Spiroceratidae*, *ioceratidae*, etc. In these the form becomes uncoiled, following out the tendencies indicated the gerontic stage of progressive forms. Their sutures are reduced to the primitive formula six, *i.e.* two pairs of zygous lateral saddles and two pairs of lobes, with a ventral and an tisiphonal; but the outlines generally remain complex even in extremely modified forms th, however, some notable exceptions like *Baculina aequarius*, Quenst. sp.

I. Psiloceratida.

Includes only one family, comprising radicals of the Jurassic Ammonoids of this b-order.

Family 1. **Psiloceratidae.** Smooth or sometimes plicated shells with keelless nters. Lateral and dorsal inflections inclined apicad as a rule, but vary considerably. ze of saddles reduced along lines of involution, but there are generally three pairs of rsal saddles. Ventral lobe shorter than in *Leptocampyli*, and siphonal saddles larger, in *Arietidae*. Aperture with a short rostrum and lateral sinuses resembling those of *rietidae*, but rostra less acute than in keeled forms.

Psiloceras has the form and shell characters of *Monophyllitidae*, and in subsequent stages

[1] The *Lenticeratidae* and *Placenticeratidae* furnish the principal exceptions, since they have the imitive first lateral saddles beginning to split at an early stage into what afterwards develop into ree pairs of practically independent lobes and saddles, whereas the primitive first lateral saddles ually persist as bifid or trifid saddles throughout life in other forms of this sub-order.

the sutures acquire phylliform marginals like those of *Phyllocampyli;* but this is not invariably the case, and characters of the dorsal and lateral sutures as well as of the shell vary in different directions. In one direction they join with *Caloceras* at the base of the present sub-order; in another they unite with *Angulatida*, as recognised by most observers; and in a third they show affinities with *Agassiceras.*

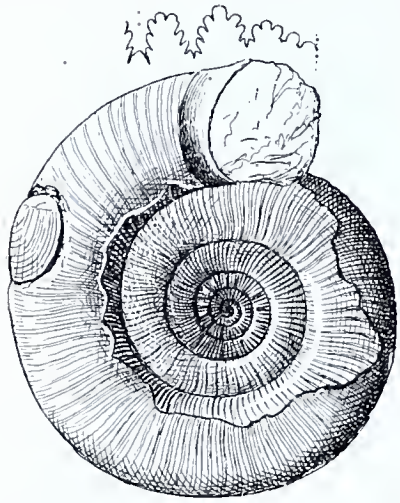


Fig. 1194.

Psiloceras planorbis, Sowb. sp. Infra-Lias; Bebenhausen, Würtemberg. Anaptychus in living chamber.

Psiloceras, Hyatt (Fig. 1194); *Parapsiloceras*, gen. nov. Type *P. (Psil.) calliphyllum*, var. *polycyclum*, Wähner. Lower Lias.

II. Angulatida.

Primitive discoidal shells indicate probable union with Psiloceras, but tend to evolve forms in which the venter is smooth, channeled, or crossed by costae at some stage of growth even when keeled. Lateral sutures more complex than in Arietida, and apt to be inclined apicad in specialised shells; dorsal sutures like those of Arietida.

Family 2. **Angulatidae.** More or less compressed and costated shells, the costae sometimes crossing the venter in the young or extreme age, but usually interrupted in the adult by a smooth and occasionally sunken median zone. Sutures inclined apicad near lines of involution, more complex in outline than in typical *Arietidae*, and with phylliform marginals more like those of *Psiloceras.* Ventral lobe broader and shorter, with larger siphonal saddles than *Arietidae*, and antisiphonal lobe bifid, longer, and more complex. First pair of dorsal saddles large and long, other dorsal inflections variable, but generally more numerous than in *Arietidae.*

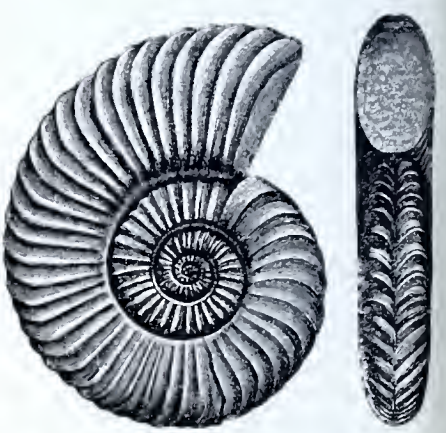


Fig. 1195.

Schlotheimia angulata, Schloth. sp. Lower Lias; Göppingen, Würtemberg.

Schlotheimia, Bayle (Fig. 1195); *Waehneroceras*, Hyatt. Lower Lias.

Family 3. **Polymorphidae.** Haug. Shells compressed discoidal, with smooth young like those of *Psiloceras.* Costae apt to be inclined or slightly sigmoidal, and continuous across the venter. This is crenulated in primitive forms, but becomes smooth, channeled, or keeled in specialised shells. The latter have sutures similar to those of *Angulatidae* and *Liparoceratidae*, but less complex. Connects with *Psiloceras* through *Gemmelaroceras.*

Polymorphites, Sutner; *Amphiceras*, Gemm.; *Uptonia*, *Tmetoceras*, Buckm.; *Gemmellaroceras*, gen. nov. Type *G. (Aegoc.) aenigmatum*, Gemm. sp. Lias and Inferior Oolite.

III. Arietida.

Primitive discoidal forms keeled and often channeled, with sides costated as in Coroniceras, etc. External sutures limited, as a rule, and auxiliaries rise orad toward lines of involution, but may be considerably extended, and number of inflections increased in highly involute shells. Dorsal sutures still more limited, and never have the monophyllic

outline common in Psiloceras. Keel solid except in the highly accelerated genus Oxynoticeras, where it is hollow.

There are two types of young in *Arietida*, which afterwards become separated in other related groups: a broad depressed or coronate type occurs in typical *Arietidae* and some others, and the compressed *Psiloceran* type in *Arnioceras*, etc. *Pseudotropitidae* show that *Coeloceras* may have originated from *Arietidae* through persistent development of a trapezoidal form of young with correlative changes.

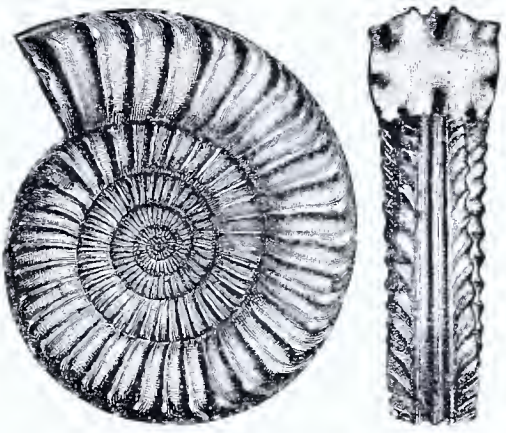


Fig. 1196.

Coroniceras bisulcatum, Brug. sp. Lower Lias; Côte d'Or (after d'Orbigny).

Family 4. **Arietidae**. Volutions of discoidal forms more quadrate than in preceding families, and often with channeled venter. Costae more strongly developed as a rule, and with prominent ventro-lateral angles, which are sometimes tuberculated. Sutural inflections reduced in number and complexity as compared with preceding families, and phylliform marginals replaced by saddles of more irregular aspect. Ventral lobe long and narrow, with corresponding siphonal saddle. Usually only two pairs of large lateral saddles, the second often the most prominent. First pair of lateral lobes large, second and third pairs successively smaller; third and fourth pairs of saddles also smaller, the last often partially on line of involution. Antisiphonal bifid, very long, and sometimes complex. One pair of large dorsal saddles, and one of short, often incomplete lobes. Anaptychus observed in several species.

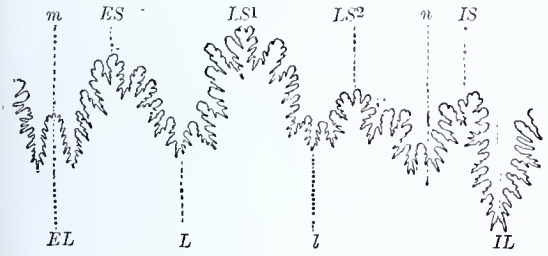


Fig. 1197.

Suture-line of *Coroniceras bisulcatum*, Brug. sp. (cf. Fig. 1097).

Coroniceras (*Arietes*, Waagen), (Figs. 1196, 1197), *Vermiceras*, *Arnioceras*, *Asteroceras*, *Tmaegoceras*, *Caloceras*, Hyatt (*Ophioceras*, Hyatt; *Alsatites*, Haug); *Echioceras*, Bayle. Lower Lias.

Family 5. **Oxynotidae**. Shells compressed and more involute than in *Arietidae*, with narrower and more acute keeled venter, but no ventral channels. Sutures Arietean in *Agassiceras*, but have extended and highly modified auxiliary inflections in *Oxynoticeras*. Keel hollow in adult of some species of the latter genus, and in a transitional condition in *Aetomoceras*.

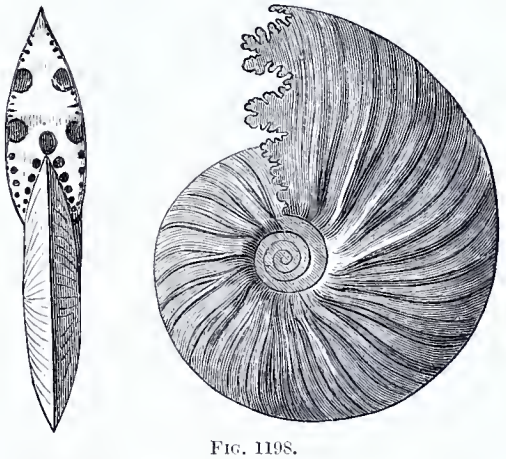


Fig. 1198.

Oxynoticeras oxynotum, Quenst. sp. Lower Lias (*β*); Würtemberg.

Oxynoticeras (Fig. 1198), *Agassiceras*, Hyatt; *Cymbites*, Neum.; (?) *Paroniceras*, Bon.; *Aetomoceras*, gen. nov. Type *A.* (*Amm.*) *scipionianum*, d'Orb. sp. Lower Lias.

Family 6. **Hildoceratidae**. Discoidal involute shells have sigmoidal costae separated throughout or confluent on the

median lateral line, and sometimes bifurcated externally. Nodes never present, although prominent crescentic ridges may arise on the sides through confluence of costae. The latter are straight in primitive *Catulloceras*, which resembles *Caloceras*

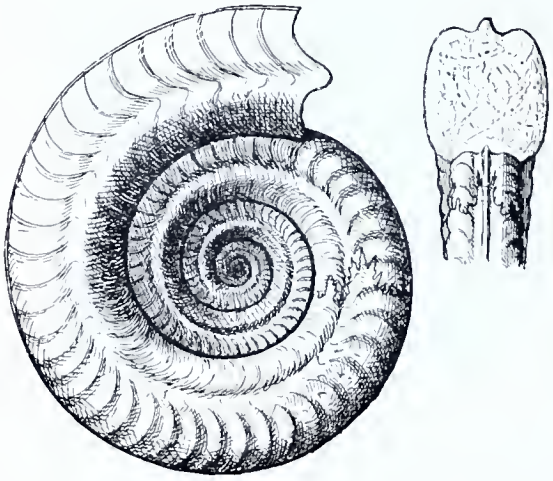


Fig. 1199.

Hildoceras bifrons, Brug. sp. Upper Lias; Whitby, Yorkshire.

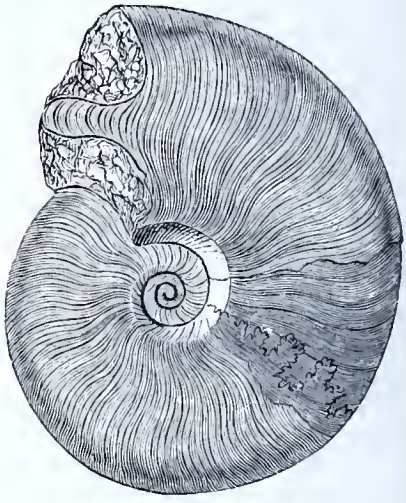


Fig. 1200.

Lioceras opalinum, Rein. sp. Lower Dogger; Teufelsloch, near Boll, Würtemberg.

in aspect. Discoidal forms often both keeled and channeled on the venter, and sometimes have broad furrows on the sides. Specialised involute shells have solid keels, but usually no channels, and lateral zones often become smooth. Sutures comparatively simple, and in discoidal forms similar to those of *Arnioceras*, but more complex in highly involute forms.

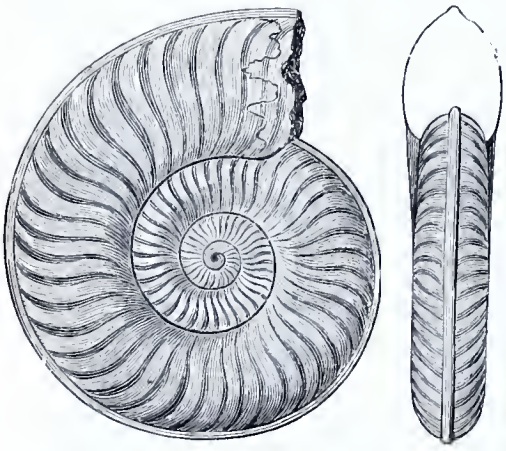


Fig. 1201.

Dumortieria, sp. Upper Lias; Heiningen, Würtemberg.

Hildoceras (Fig. 1199), *Lioceras* (Fig. 1200), *Grammoceras*, Hyatt; *Catulloceras*, Gemm.; *Dumortieria*, Haug (Fig. 1201); *Arieticeras*, Seg.; *Hyperlioceras*, *Graphoceras*, *Brasilia*, *Darellia*, Buckm. Upper Lias and Inferior Oolite.

Family 7. **Poecilomorphidae.** Costae in some species remain nodose on umbilical shoulders until a late stage, and bifurcate externally as in *Oppelidae*, but subsequently may become separated into single sigmoidal ridges like those of *Hildoceratidae*. Young similar to those of the latter family, and sutures also in discoidal forms, but become more complex in involute shells.

Poecilomorphus, *Huddlestonia*, *Brodieia*, *Cosmogyria*, *Welschia*, Buckman; *Ludwigia*, Bayle. Inferior Oolite.

Family 8. **Oppelidae.** (*Oppelinae*, Haug.) Discoidal and highly involute shells with sutures, form, and markings in primitive species that show affinity with Hildoceran stock, and apparent derivation from *Poecilomorphus* through typical *Oecotraustes*. Costae highly flexed and sometimes fused, but no well-marked lateral channels as in hollow-keeled groups. Venter often truncated and sides flattened, except in primitive

species. Keel may become very prominent and filled with special shell-layers, but never hollow. Young generally smooth, compressed, and similar to those of *Hildoceratidae*.

Oecotraustes, *Oppelia* (Fig. 1100), Waagen; *Hectioceras* (*Lunuloceras*), Bonar. Middle Jura.

IV. Phymatoida.

Similar to Arietida in that each family includes some discoidal radical forms having keels and channels. Volutions generally stouter, costae coarser and larger, and also more apt to become bifurcated and to develop nodes. Young generally pass through a nodose coronate stage. Keel hollow in the adult, but solid in the young, extreme age, and in primitive forms. Connection with Oxynoticeras improbable, since the hollow keel appears to have arisen independently.

Family 9. **Amaltheidae**. Buckman, p.p. Discoidal and involute shells, the young of which have fold-like costae rising into heavy nodes just inside the lines of involution. Costae become prominent and sharp at umbilical shoulders and ventro-lateral angles, and true tubercles appear in some Zurcherinae. Venter keeled and sulcated in discoidal forms, the keels alone persisting in more involute species. Keel solid and crenulated by passage of costae or folds across the venter. Anaptychus present.

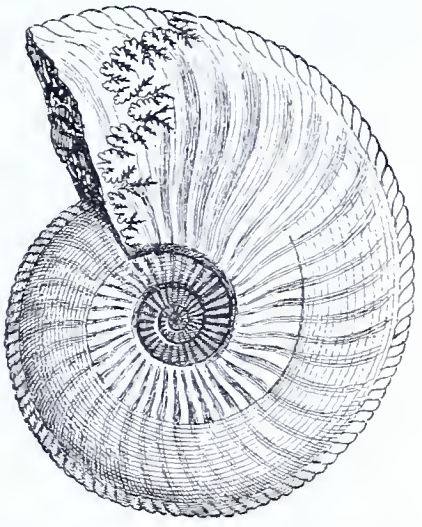


Fig. 1202.

Amaltheus margaritatus, Montf. Middle Lias; Würtemberg. Living chamber broken away and exposing "wrinkled layer" on ventral surface. This is homologous with the "black layer" of *Nautilus*.

A. Amaltheinae. Nodes prominent in young of primitive species; costae with only one row of tubercles in later stages or none: keel invariably present and crenulated. *Amaltheus*, Montf. (Fig. 1202); *Paltopleuroceras*, Buckm. (*Pleuroceras*, Hyatt). Middle Lias.

B. Zurcherinae. Young usually have gibbous volutions with a single row of nodes, which either persist, or are followed by a bispinous stage, and inner ends of the short costae also become tuberculated. Venter smooth at first, and may remain so or have a solid keel. Costae single, and usually bend at ventro-lateral angles toward the keel, but do not cross the venter except in late stage of *Pseudotropites*. *Zurcheria*, *Haplopleuroceras*, *Dorsetensia*, Buckm.; *Pseudotropites*, Canav.; *Canavarites*, g. nov. Type *C.* (*Ariet.*) *diseretum*, Canav. sp. Lias to Inferior Oolite.

Family 10. **Phymatoidae**. Discoidal forms with single or bifurcated costae, keeled and often channeled venters. Young similar to those of *Hildoceratidae* and *Poecilomorphidae* in compressed forms. Keel hollow.

Phymatoceras, *Hammatoceras*, Hyatt; *Lillia*, Bayle; *Haugia*, *Polyplectus*, *Chartronia*, *Denckmannia*, Buckm.

The type of *Phymatoceras* is *Amm. Tirolensis*, Dumortier, the so-called *P. robustum*, Hyatt, having proved to be identical with the young of that species. Upper Lias and Inferior Oolite.

Sub-Family Sonninae. Buckman. *Sonninia* includes discoidal forms with keeled but not channeled venter, and sides with coarse bifurcated costae diverging from a row of nodes along the median line of the rounded sides, and continued internally by single costae. *Witchellia* has nodes only in the young, and costae become single or

only slightly confluent. *Sonninia* (*Waagenia*, Bayle), (Fig. 1203); *Witchellia*, Buckman. Inferior Oolite.

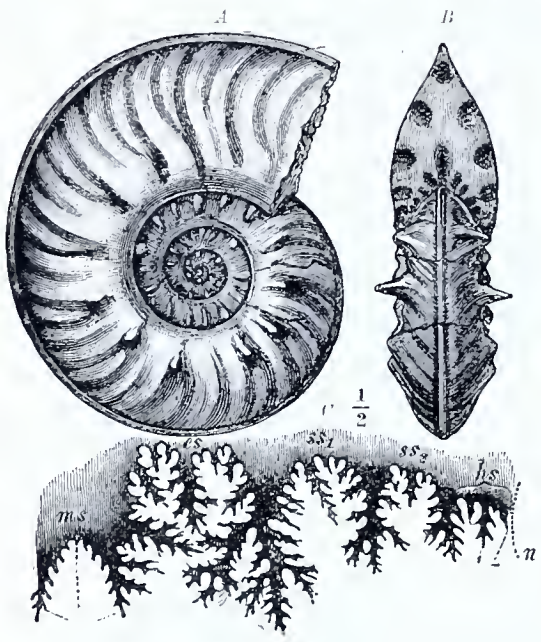


Fig. 1203.

Sonninia Sowerbyi, Miller sp. Middle Dogger; Lorraine (after Steinmann and Doderlein).

V. Liparoceratida.

Discoidal radical forms have more or less subquadrate volutions with coarse, fold-like, single, or bifurcated costae continuous across the venter. External and dorsal sutures limited in number of inflections as in Arietidae, but development of marginals carried to utmost degree of complexity in this sub-order. Keel solid when present. Two rows of large nodes or spines sometimes developed on either side.

Family 11. **Liparoceratidae.** Volutions remain rounded in section and frequently retain a primitive discoidal aspect. Costae almost entirely disappear on the venter of some forms, but form very large continuous folds in others. Sutures become excessively complex, saddles narrow and deeply cut by complex marginals, and ventral lobe corresponds, but usually of about equal length with the lateral lobes. Antisiphonal bifid, and resembles (as do also the two dorsal saddles and small dorsal lobes) those of *Arietidae*.

Liparoceras, *Microderoceras*, *Amblycoceras* (*Microceras*), Hyatt (Fig. 1204); *Androgynoceras*, Hyatt. Lower and Middle Lias.

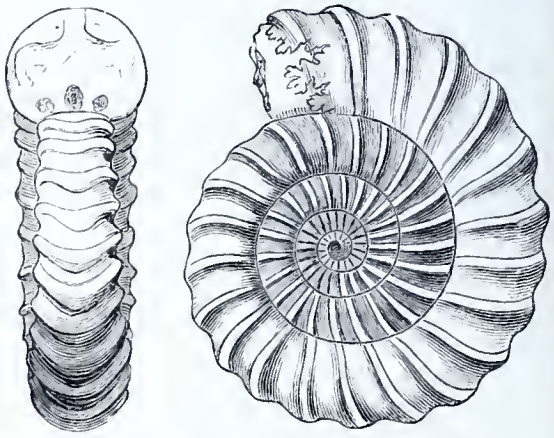


Fig. 1204.

Amblycoceras capricornus, Schloth. sp. Middle Lias; Gmünd, Würtemberg.

Family 12. **Tropidoceratidae.** Discoidal compressed shells with straight costae that cross the venter in some forms approximating to *Amblycoceras*, but usually this region is distinctly elevated, and smooth or keeled along the median zone. Costae have two rows of tubercles in several species, but may be smooth in others. Sutures similar to those of *Uptonia*, but more complex; lobes, however, exceedingly narrow and auxiliary line inclined apicad. Dorsal sutures like those of *Amblycoceras bifer*.

Tropidoceras (*Harpoceras*, Waagen), *Platypleuroceras*, Hyatt; *Acanthopleuroceras*, nom. nov. Type *A.* (*Amm.*) *natrix*, Schloth. sp. [The latter name is substituted for *Cycloceras*, Hyatt, preoccupied among Nautiloids.] Middle Lias.

VI. Dactylioida.

Young have volutions with trapezoidal sections, venter broader than dorsum and decidedly coronate, or with a line of nodes along the ventro-lateral angles, and broad

umbilical but no true lateral zones. Some genera have the latter condition persistent throughout life. Costae apt to be continuous across the venter even in specialised forms with both channels and keels. Some genera, however, have costae divided on the venter or suppressed, but there is no continuous median channel. Keel solid when present.

Family 13. **Dactylioidae**. Discoidal forms with costae bifurcated and always crossing the venter. Sutures with very complex outlines, but only three or four pairs of lateral lobes and saddles. Dorsal sutures have two pairs of saddles and one pair of zygous lobes.

This series is usually termed the *Planulati* of the Lias, but although an offshoot of the same common stock it is quite distinct from its supposed congeners of the Middle and Upper Jura. Sutures are straight, not inclined apicad as in *Perisphinctidae*. The family comprises a complete cycle of forms varying from the broad trapezoidal, tuberculated volutions of *Coeloceras* through Armatoid species to *Dactylioceras*, in which the costae are smooth and sometimes even single.

Coeloceras, *Deroceras* (Fig. 1205), *Dactylioceras* (Fig. 1206), *Peronoceras*, Hyatt; *Pimelites*, *Diaphorites*, Fucini; (?) *Praesphaeroceras*, Levi; (?) *Collina*, Buckm. Middle and Upper Lias.

Family 14. **Stepheoceratidae**. Buckman. Primitive radicals, highly coronate, discoidal, giving rise apparently to involute and partially compressed forms that in

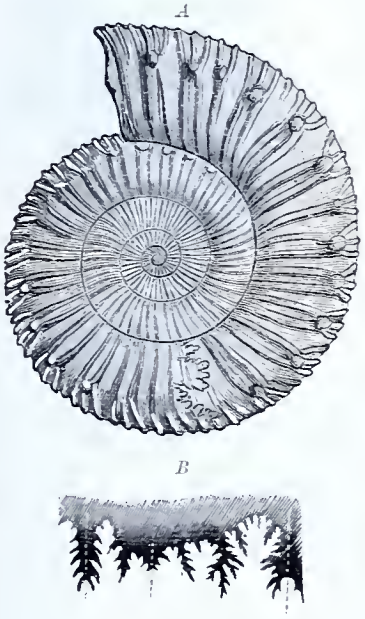


Fig. 1205.

A, *Deroceras subarmatum*, Young sp. Whitby, Yorkshire. *B*, Suture-line of *Coeloceras pettos*, Quenst. Middle Lias.

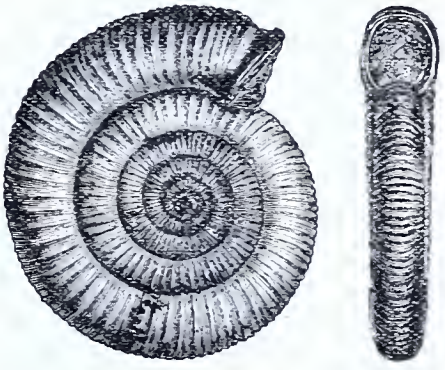


Fig. 1206.

Dactylioceras commune, Sowb. sp. Upper Lias; England.

Fig. 1207.

Sphaeroceras Brongniarti, Sowb. sp. Inferior Oolite; Bayeux, Calvados.

Macrocephalites and some others are without tubercles. Venter always rounded, costae bifurcating on the sides and continuous across the venter. Only one line of nodes or tubercles at the umbilical shoulders, and division of costae takes place along these lines in most forms. Sutures of the same type as in *Dactylioidae*, but much more complex, with usually more inflections, and lobes and saddles more nearly equal. Dorsal sutures generally have three pairs of zygous saddles and two pairs of lobes in coronate discoidal forms.

Stepheoceras, Buckman (*Stephanoceras*, Neum.; *Cadomites*, Mun.-Chalm.); *Sphaeroceras*, Bayle (Fig. 1207); *Emileia*, Buckman; *Normannites*, Mun.-Chalm. (Fig. 1208); *Maeroecephalites*, Sutner (Fig. 1209); *Sutneria*, Zittel (Fig. 1210); *Erymnoceras*, gen. nov. (Fig. 1211). Type *E.* (*Amm.*) *coronatum*, Brug. sp. Inferior Oolite.

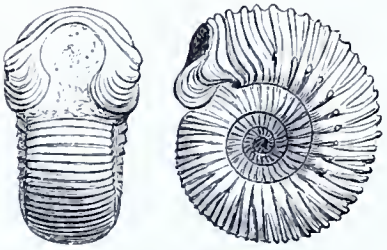


Fig. 1208.

Normannites Brailsfordi, Sowb. sp. Inferior Oolite; Bayeux, Calvados. 1/1.

Family 15. **Cadoceratidae.** More specialised, compressed, and involute forms tend to evolve shells with crenulated keels, and sometimes channels also. Costae of *Cadoceras* divided as in *Stepheoceratidae*, but other genera usually develop two lines of tubercles. Young of *Neumayria* more or less costated, but sides and keel become smooth, and in some species resemble adult of *Quenstedtoceras*.

This family is remarkable for the close parallelism of some of its genera with *Amaltheidae*, but the young are very distinct. Development and adult stages of *Cadoceras* with its discoidal

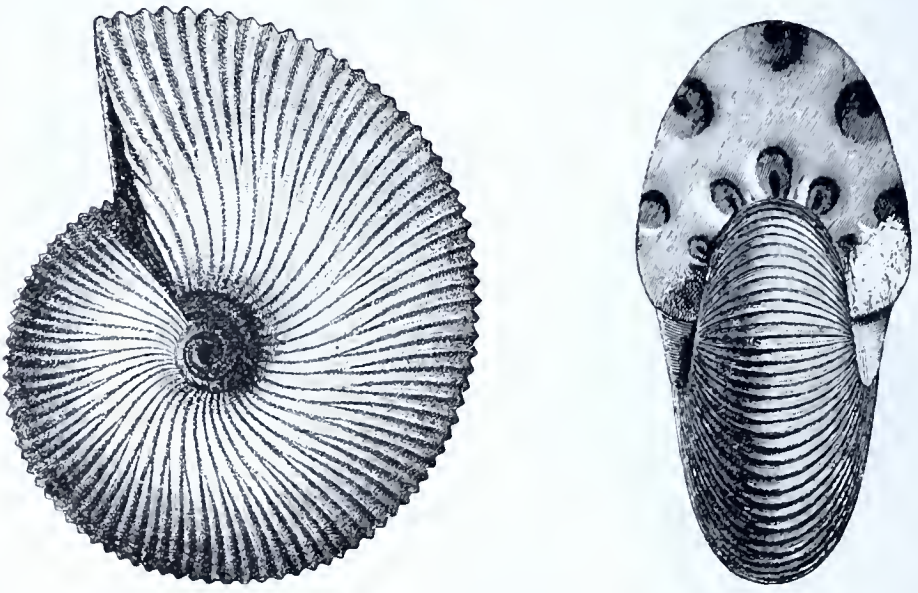


Fig. 1209.

Macrocephalites macrocephalus, Schloth. sp. Upper Dogger (Callovian), Ehningen, Würtemberg.

and much depressed volutions plainly show derivation from Coeloceran stock, while its form and sutures also show relationship with *Stepheoceratidae*.

Cadoceras, Fischer; *Quenstedtoceras*, Hyatt; *Cardioceras*, Neum. and Uhlig; *Neumayria*, Nikitin; *Amoebocerας*, gen. nov. Type *A.* (*Amm.*) *alternans*, von Buch sp. Kelloway.

Family 16. **Perisphinctidae.**[1] An extensive series of discoidal genera having rounded or subquadrangular volutions, and costae single on the sides, but split into two, three or more on the venter, which they cross uninterruptedly. Splitting does not begin as a rule at umbilical shoulders, but near ventro-lateral

Fig. 1210.

Sutneria platynotus, Rein. sp. Upper Jura (*Tenuilobatus* Beds); Balingen, Würtemberg.

[1] *Siemiradzki, J.*, Monographische Beschreibung der Gattung Perisphinctes (Palaeontogr. Bd. XLV.), 1898.

angles. Inner parts of sutures steeply inclined apicad, and dorsal sutures have a long

Fig. 1211.

Erymnoceras coronatum, Brug. sp. Callovian; Dept. Nièvre, France. 1/3.

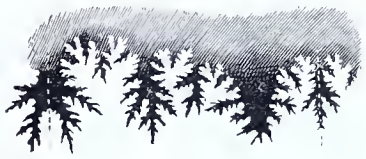


Fig. 1212.

Suture-line of *Perisphinctes colubrinus*, Rein. sp.

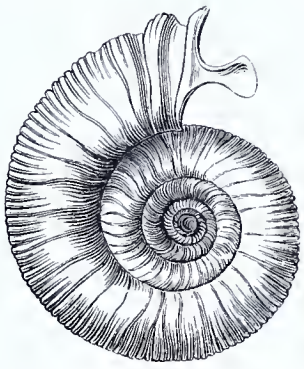


Fig. 1213.

Perisphinctes polyplocus, Rein. sp. Upper Jura; Pappenheim, Bavaria. 1/2.

pair of first dorsal saddles, usually two additional pairs of saddles, and two pairs of lobes. All of these are so decidedly inclined apicad that they often appear as a single pair of complex saddles.

These genera are morphic equivalents of the Liassic *Dactylioidae* and are derived from the same common stock. Young have depressed trapezoidal volutions and often minute tubercles on ventro-lateral angles, but are otherwise smooth, like the young of *Cadoceras sublevc*. They become compressed in neanic stage and rapidly assume the discoidal Perisphinctean form and costae without tubercles.

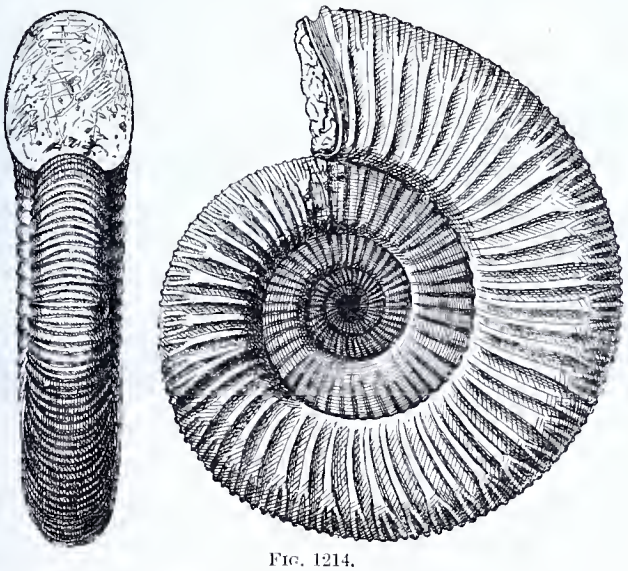


Fig. 1214.

Perisphinctes Tiziani, Oppel sp. Upper Jura (*Bimammatus* Beds); Hundsrück, near Streichen, Würtemberg.

Perisphinctes, Waagen (*Grossouvria*, *Procerites*, *Choffatia*, Siemirad.) (Figs. 1212-1214); *Ataxioceras*, Font.; *Proplanulites*, Teiss.; *Pictonia*, Bayle; *Craspedites*, Pavl. and Lampl.; *Lithacoceras*, gen. nov. Type *L.* (*Amm.*) *Ulmensis*, Oppel sp. Inferior Oolite and Cretaceous.

Family 17. **Aspidoceratidae.** Zittel, p.p. Earlier volutions costated, later ones with one or two rows of tubercles, the inner row being developed first. Venter broad, never keeled. Sutures resemble those of *Dactylioidae*, but saddles and lobes broader and dorsal sutures with only one large pair of inner or first dorsal

lobes, the outer or second pair being incomplete in the more discoidal species as

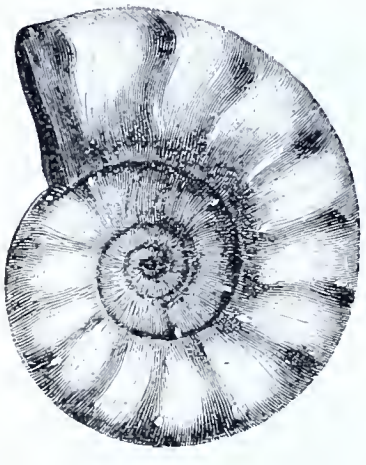


Fig. 1215.

Aspidoceras perarmatum, Sowb. sp. Oxfordian; Dives, Calvados. 1/2.

Fig. 1217.

Simoceras Volanense, Oppel sp. Lower Tithonian; Monte Catria, Central Apennines.

in *Arietidae*. *Siemiradzkia* bears resemblance in the young or throughout life to *Perisphinctes*.

Aspidoceras, Zittel (Fig. 1215); *Peltoceras*, Waagen (Fig. 1216); (?) *Aurigerus*, Oppel; (?) *Simoceras*, Zittel (Fig. 1217); *Siemiradzkia*, gen. nov. Type *S.* (*Amm.*

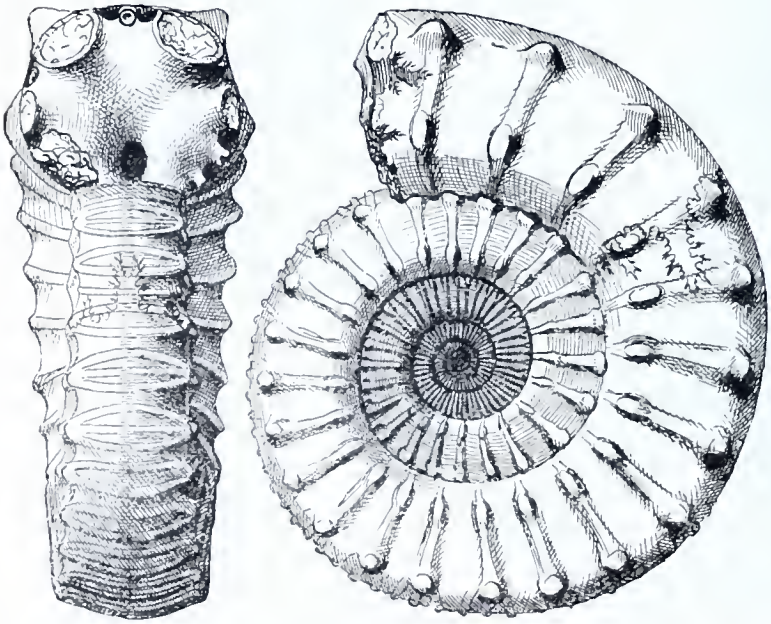


Fig. 1216.

Peltoceras athleta, Phill. sp. Upper Callovian; Vaches noires, Normandy. 1/1.

Fig. 1218.

Physodoceras circumspinosum, Oppel sp. Upper Jura; Swabian Alps. 1/2.

Bakeriae, d'Orb. sp. [*Terr. Jurass.* Pl. 149, Fig. 1 *non* Pl. 148]. *Physodoceras*, gen. nov. (Fig. 1218). Type *P.* (*Amm.*) *circumspinosum*, Oppel sp. Upper Jura.

VII. Morphoceratida.

Some families resemble Dactylioida and have similar young, the only constant distinction being the presence of a smooth zone along the median plane of the venter. Other families very like Cosmoceratidae, but their coronate young and sometimes highly coronate adults appear to place them in this series.

Family 18. **Morphoceratidae.** Globose and usually involute forms with open umbilici showing young to be highly coronate until a late stage. Costae on umbilical zones single and widely separated, but divide into very broad bundles of fine, closely-set ventro-lateral costae differing from those of all other groups except some *Perisphinctidae*. Only one line of tubercles or nodes, which usually occur at umbilical shoulders. External and dorsal sutures resemble those of *Perisphinctidae*, but not so uniformly inclined apicad. In discoidal coronate shells the lobes and saddles are of equal length, and dorsum has two pairs of zygous lobes and two pairs of saddles.

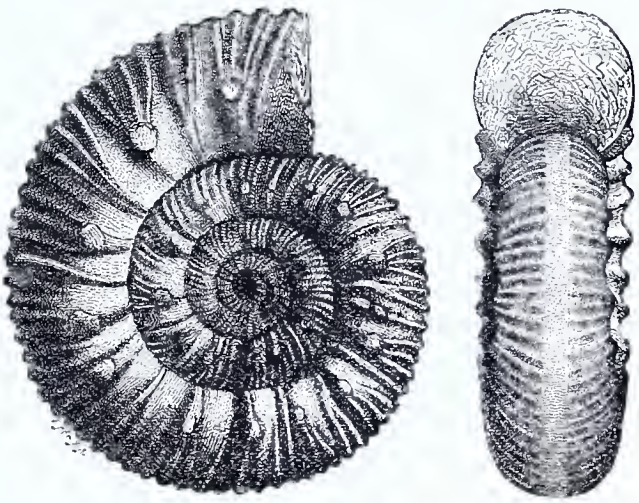


Fig. 1219.

Reineckia Brancoi, Steinm. Caracoles, Bolivia (after Steinmann).

Morphoceras, Douv.; *Garantiana*, Siemirad.; *Olcostephanus* (*Holcostephanus* auct.), Neum.; *Polyptychites*, *Simbirskites*, *Astieria*, *Virgatites*, Pavl. and Lampl. Upper Jura and Cretaceous.

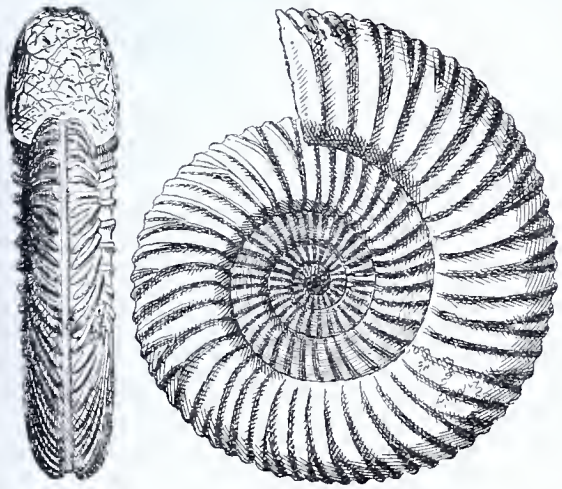


Fig. 1220.

Parkinsonia Parkinsoni, Sowb. sp. Inferior Oolite; Bayeux, Calvados.

Family 19. **Reineckidae.** Discoidal shells with costae single on the lateral zones but bifurcated on their outer parts, and with one or two lines of tubercles, the first being near the point of bifurcation of the costae, and the other near their ventral termini. Division of costae takes place along ventro-lateral angles and not on or near the umbilical shoulders. Costae cross the venter only in the coronate young, when section is trapezoidal as in *Coeloceras*. Sutures as in preceding family.

Fig. 1221.

Oecoptychius refractus, de Haan sp. Callovian; Niort, France (after d'Orbigny).

Reineckia (Fig. 1219), *Parkinsonia* (Fig. 1220), Bayle; *Oecoptychius*, Neum. (Fig. 1221); *Aulacostephanus*, Sutner and Pomp.; (?) *Waagenia*, Neum., *Strenoceras*, gen. nov. Type *S.* (*Amm.*) *niortense*, d'Orb. sp. Middle and Upper Jura.

Family 20. **Spiroceratidae.** Phylogerontic, uncoiled, and straight forms, probably derived from some of the preceding family. Young are attenuated cones with single straight costae, but have four rows of tubercles at an early stage and a concave zone along the venter. Sutures of Reineckian type, but reduced to the phylogerontic formula of six lobes.

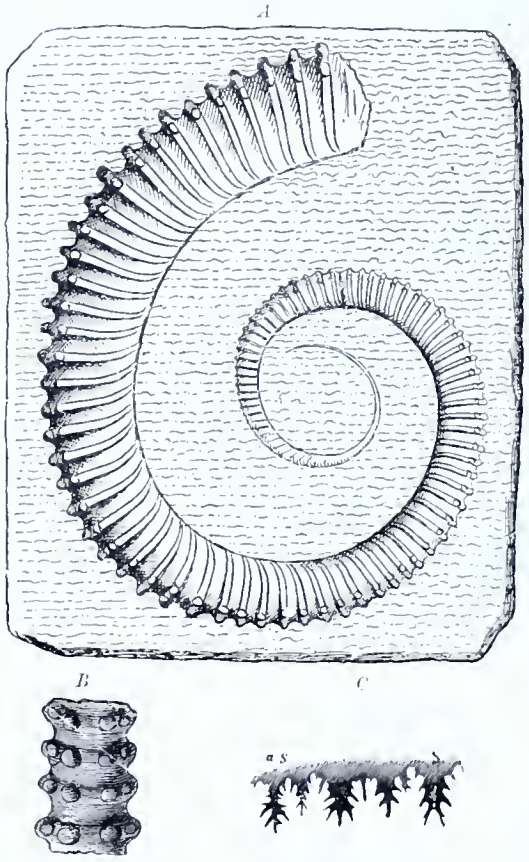


Fig. 1222.

Spiroceras bifurcatum, Quenst. sp. Upper Dogger (Callovian); Ehningen, Würtemberg. *A*, Shell with protoconch broken away, 1/1. *B*, Portion of venter. *C*, Suture-line.

Spiroceras, Quenst. (Fig. 1222); *Apsorroceras*, gen. nov. Type *A.* (*Ham.*) *baculatus*, Quenst. sp. Inferior Oolite. Incertae sedis: *Baculina*, d'Orb. Oxfordian and Neocomian.

Family 21. **Hoplitidae.** Discoidal and involute forms with costae bifurcated on the sides at umbilical shoulders; prominent tubercles at their forks, and also at or near their ventral termini, these last being separated by a median zone or deep channel. Young of some species have costae continuous across the venter, and resemble those of *Sonneratia*. Parallelism with *Cosmoceratidae* very close. Sutures resemble those of *Mammitidae*, but more complex. Lateral saddles narrower and more deeply cut, and first lateral saddles often trifid in late stages. Dorsal series with two pairs of complex zygous lobes and saddles on either side of a long, narrow, complex, antisiphonal lobe.

Fig. 1223.

Hoplites tuberculatus, Sowb. sp. Gault; Folkestone, England. Siphuncle broken away.

Hoplites, Neum. (Fig. 1223); *Cenomanites*, Haug (*Discoceras*, Kossmat); *Sonneratia*, Bayle; *Anahoplites*, gen. nov. Type *A.* (*Amm.*) *splendens*, d'Orb. sp. Cretaceous.

VIII. Placenticeratida.

Young, smooth, and compressed, with flat or concave venter, which may subsequently become acute, or remain flat throughout life, or may even become keeled. Outline apt to be rounded in old age; sides may have as many as three rows of tubercles, but in most forms are not highly ornamented. Sutures remarkably complex in some families, but in others extremely simple, recalling those of Triassic genera. General tendency is to extend

the sutures internally, and to multiply number of lobes and saddles in proportion, both externally and on the dorsum. First lateral saddles apt to divide in later stages into three distinct saddles.

Family 22. **Sphenodiscidae.** Sutures slightly more complex than those of *Engonoceratidae*, and with phylliform marginals; dorsals monophyllic. Young similar to those of *Engonoceratidae* in primitive species, and have concave venters and compressed volutions. Venter subacute or keeled in the adult, but later loses its keel, and becomes plano-convex or rounded.

Sphenodiscus, Meek; *Indoceras*, Noetling; *Libycoceras*, gen. nov. (Fig. 1224). Type *L.* (*Sphen.*) *Ismaëli*, Zittel. Cretaceous.

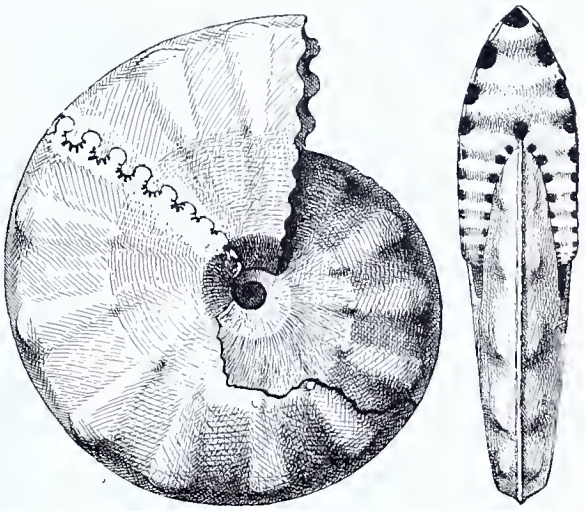


Fig. 1224.

Libycoceras Ismaëli, Zittel sp. Upper Senonian; Libyan Desert west of Oasis Dachsel.

Family 23. **Placenticeratidae.** Tuberculated and smooth forms, the young of which pass through a stage with smooth, flat, or concave venters similar to adult of *Engonoceras*. Venter remains flat or compressed until old age, when it becomes rounded. Sutures remarkable for their complex, irregular, ragged outlines, and narrowness of saddles. Their outlines in the young very similar to those of *Sphenodiscidae*.

Placenticeras, Meek; *Diplacomoceras*, gen. nov. Type *D.* (*Amm.*) *bidorsatus*, Schlüt. sp. Cretaceous.

Family 24. **Engonoceratidae.** Compressed shells with numerous saddles and concave or flat venter. Costae nodose in some species, but usually fold-like and sometimes merely broad, low lateral swellings. Sutures simpler than in *Sphenodiscidae*, but of the same type.

Engonoceras, Neum.; *Knemiceras*, Böhm; *Neolobites*, Fischer; *Protengonoceras*, gen. nov. Type *P.* (*Amm.*) *Gabbi*, Hyatt = *Amm. pedernalis*, Gabb. Cretaceous.

IX. Acanthoceratida.

A series of more or less uncoiled genera connected through the transitional Acanthoceratidae with normal Cretaceous shells having costae interrupted on the venter at some stage or throughout life, although in most forms continuous during later stages of the ontogeny.

Family 25. **Acanthoceratidae.** Young slender, discoidal, without tubercles, and section rounded until late in neanic stage. Sutures have deeply-cut outlines, and owing to frequent presence of only six lobes and saddles simulate those of *Leptoceampyli*, but are not of the same type. First lateral saddles broad and bifid; ventral lobe straight, deep, and has a truncated siphonal saddle. External characters similar to some forms of *Hoplitidae*. Some species have costae bifurcated, more or less interrupted, and with only the ventro-lateral row of tubercles or none.

Acanthoceras, Neum.; *Thurmannia*, gen. nov. Type *T.* (*Amm.*) *Thurmanni*, Pict.

and Camp.; *Lyticoceras*, gen. nov. (Fig. 1225). Type *L.* (*Amm.*) *eryptoceras*, d'Orb. sp.; (*?*) *Vascoceras*, Choff.[1] Cretaceous.

Family 26. **Hamitidae.** A provisional group of uncoiled shells having single costae crossing the venter uninterruptedly, and no tubercles at any stage.

Hamites, Park.; *Hemibaculites*, gen. nov. Type *H.* (*Toxoc.*) *obliquatum*, d'Orb. sp.; *Dirrymoceras*, gen. nov. Type *D.* (*Ancyl.*) *simplex*, d'Orb. sp.; *Torneutoceras*, gen. nov.

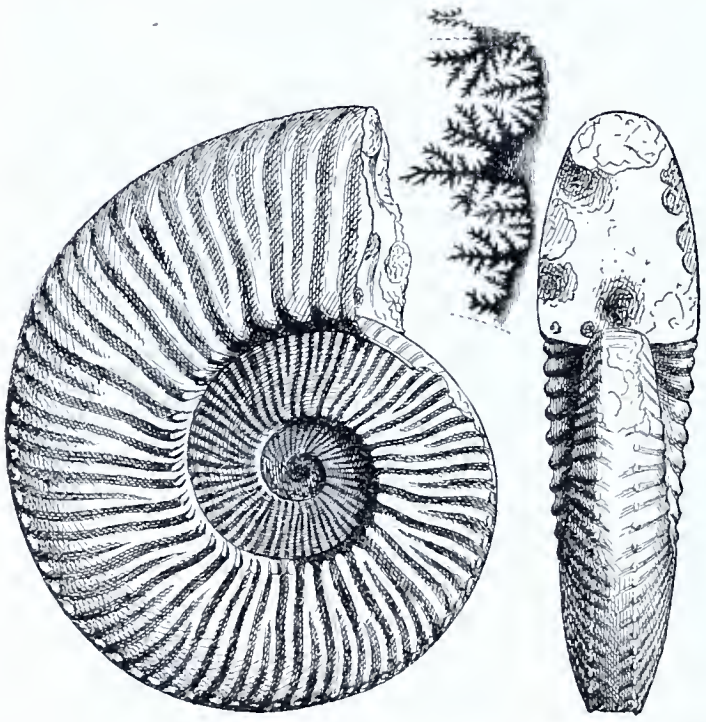


Fig. 1225.

Lyticoceras Noricum, Sowb. sp. (=*Hoplites amblygonius*, Neum.). Neocomian; Achim, near Börsum, Prussia.

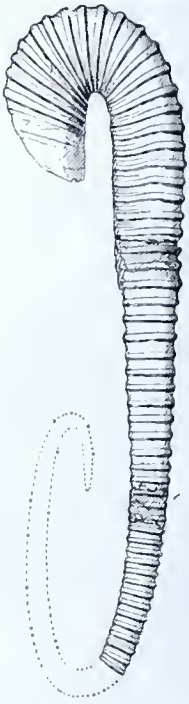


Fig. 1226.

Torneutoceras rotundatum, Sowb. sp. Gault; Folkestone.

(Fig. 1226). Type *T.* (*Ham.*) *attenuatus*, d'Orb. sp. Possibly here also should be placed *Helicoceras* and *Heteroceras*, d'Orb.; and *Lindigia*, Karstens—all asymmetrical spirals, but in old age forming a secondary crook striking off from the spire. Cretaceous.

X. Cosmoceratida.

Highly tuberculated and costated forms having a smooth zone on the venter or costae extending across it, but never with a line of median ventral tubercles nor a keel at any stage. Numerous phylogerontic uncoiled forms occur in the Cretaceous.

Family 27. **Cosmoceratidae.** Discoidal and involute forms having at a comparatively early stage or throughout life two or three rows of large tubercles on each side, and costae interrupted on the venter by a smooth median zone or channel.

Late stages of all genera except *Cosmoceras* and *Phricodoceras* have costae continuous across the flattened venter, and species of the latter indicate possible transitions to *Amblycoceras*. All forms have a Cosmoceran stage quite distinct from the young of *Morphoceratidae*.

[1] *P. Choffat*, Recueil d'études paléontologiques sur la faune crétacique du Portugal, Les Ammonées du Bellasien, etc. Lisbonne, 1898.

Cosmoceras, Waagen (Fig. 1227); *Phrieodoceras*, gen. nov. Type *P.* (*Amm.*) *Taylori*, d'Orb. sp.; *Sigaloceras*, gen. nov. Type *S.* (*Amm.*) *calloviense*, d'Orb. sp. Middle Lias to Oxfordian.

Family 28. **Pedioceratidae.** Young resemble *Cosmoceratidae*, but later the large single or imperfectly bifurcated costae are apt to cross the venter. Sometimes all traces of tubercles are lost, but most forms possess until a late stage a row on the ventro-lateral angles, another in juxtaposition to this externally, and either two more or none inside these rows.

Pedioceras, Gerh.; *Douvilleiceras*, Gross. (Fig. 1228); *Steueroceras*, Cossm. (*Odontoceras*, Steuer); *Diadochoceras*, gen. nov. Type *D.* (*Amm.*) *nodosocostatum*, d'Orb. sp. Cretaceous.

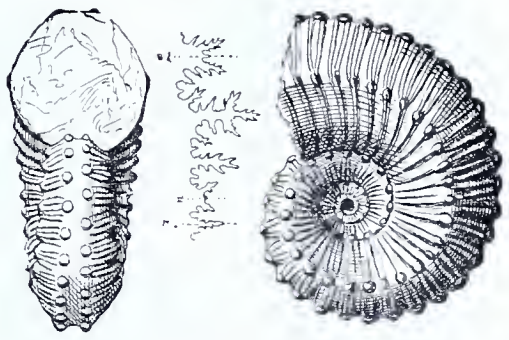


Fig. 1227.

Cosmoceras ornatum, Sowb. sp. Callovian (Ornatenthon); Gammelshausen, Würtemberg.

Family 29. **Anisoceratidae.** Uncoiled shells with only two rows of tubercles on either side, and costae similar to those of preceding family. The adult *Anisoceras* has a Helicoceran aspect, develops a long, eccentric *Toxoceras*-like volution in the gerontic stage, and terminates with a retroversal bend or crook.

Anisoceras, Pict.; *Tonoceras*, gen. nov. Type *T.* (*Aneyl.*) *Duvalianum*, d'Orb. sp.; *Hyphantoceras*, gen. nov. Type *H.* (*Heteroc.*) *Roissyanum*, Schlüt. sp. Cretaceous.

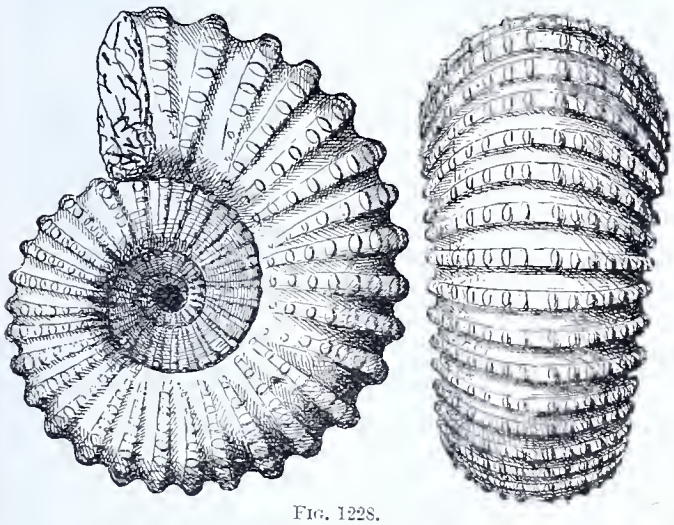


Fig. 1228.

Douvilleiceras mamillare, Schloth. sp. Gault; Macheromenil, Ardennes.

Family 30. **Turrilitidae.** Turriliticones having more or less angulated volutions, with two rows of tubercles on either side of the median line of the venter. Shells close-coiled from the earliest stage, or with only a slight eccentric deviation in old age; often partially costate, and sometimes with only three rows of tubercles in older stages. Aperture much elongated transversely, and contracted in extreme age of *Turrilites* by ingrowth of the right side. Costae continuous across the venter or interrupted by a smooth zone, and either single or divided between the rows of tubercles.

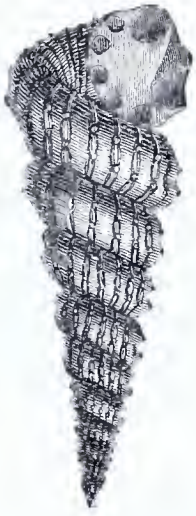


Fig. 1229.

Turrilites catenatus, d'Orb. Gault; Escragnolles, France (after d'Orbigny).

Turrilites, Lam. (Fig. 1229); *Ostlingoceras*, gen. nov. Type *O.* (*Turr.*) *Puzosianum*, d'Orb. sp. Cretaceous.

Family 31. **Ancyloceratidae.** Includes only such forms usually assigned to

Ancyloceras, *Crioceras*, etc., as have three rows of tubercles on either side on the larger costae. Between the latter are smaller costations without tubercles. Costae sometimes interrupted across the venter by a smooth zone.

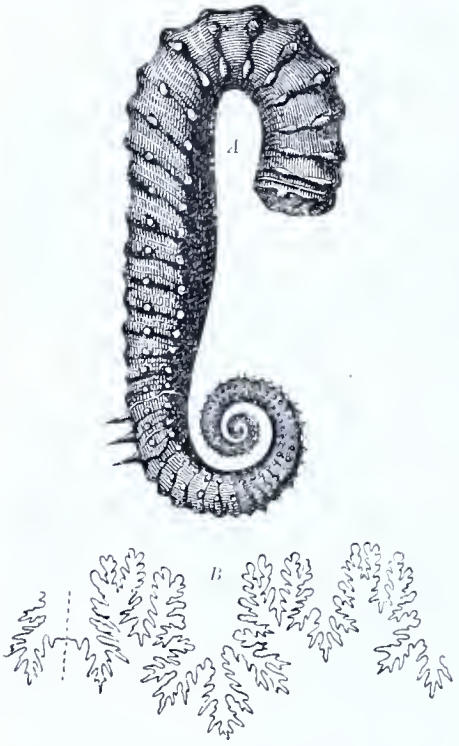


Fig. 1230.

Ancyloceras Matheronianum, d'Orb. Neocomian; Castellane, Basses Alpes. *A*, Conch. *B*, Suture-line.

Ancyloceras (Fig. 1230), *Hamulina*, d'Orb. (Type *H. dissimilis*, d'Orb.); *Pictetia*, Uhlig; *Helicancylus*, Gabb; *Distoloceras*, gen. nov. Type *D.* (*Hopl.*) *hystrix*, Neum. and Uhlig sp.; *Acrioceras*, gen. nov. Type *A.* (*Ancyl.*) *Tabarelli*, Astier sp. Cretaceous.

Family 32. **Crioceratidae**. Volutions more or less roughened and costated, with only two lines of tubercles on either side of the median line of the venter. The latter may have a smooth zone or be crossed by the costae, which are either single or double between the tubercles.

Fig. 1231.

Bostrychoceras polyplocum, Roemer sp. Upper Cretaceous; Haldem, Westphalia.

Crioceras, d'Orb. (*Crioceratites*, Lev.); *Oxybeloceras*, gen. nov. Type *O.* (*Pty.*) *crassum*, Whitf. sp. Cretaceous.

Family 33. **Nostoceratidae**. Adult spirals asymmetrical turriliticones, with more or less prominent costae and one row of tubercles on each side of the venter. Extreme gerontic stage often retroversal, the return being in some cases complete, so that aperture is brought close against base of the spire. Young of *Emperoceras* may remain Hamitean for a prolonged period, and then suddenly become Helicoceran or turrilitiform.

Nostoceras, *Emperoceras*, *Didymoceras*, *Exiteloceras*, Hyatt; *Bostrychoceras*, gen. nov. (Fig. 1231). Type *B.* (*Heteroc.*) *polyplocum*, Schlüt. sp. Cretaceous.

XI. Mammitida.

Shells closely paralled to Cosmoceratida, but differ in having at some stage a median line of tubercles along the venter. These are fused in more specialised genera into a solid entire keel.

Family 34. **Mammitidae**. Differ from *Pedioceratidae* in that the venter is rounded and smooth in the young, after which a median ventran row of tubercles appears, or a keel resulting from their fusion. Sutures have larger and more solid saddles than in *Pedioceratidae*, and first lateral saddles generally bifid.

Mammites, Laube and Bruder; *Muniericeras*, Gross.; *Barroisiceras*, Gross.;

Calycoceras, gen. nov. Type *C.* (*Amm.*) *navicularis*, Sharp sp.; *Metacanthoplites*, gen. nov. (Fig. 1232). Type *M.* (*Amm.*) *rhotomagensis*, d'Orb sp. Cretaceous.

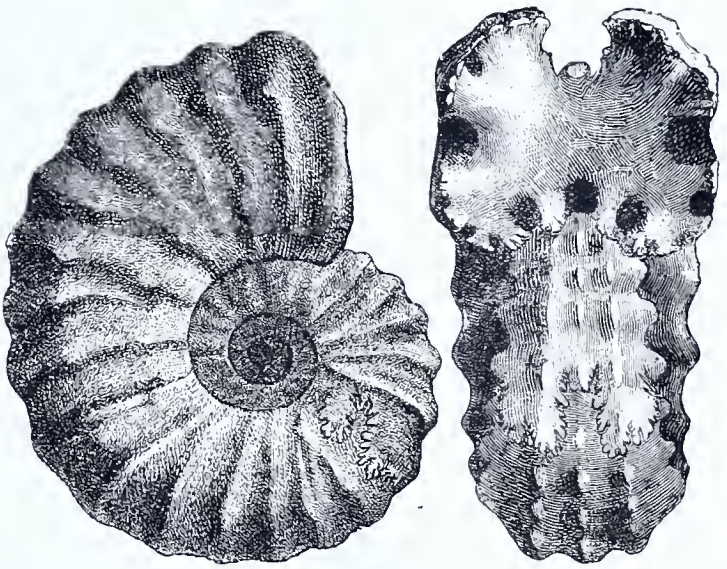


Fig. 1232.

Metacanthoplites Rhotomagense, Defr. sp. Cenomanian; Rouen, France (after Quenstedt).

Family 35. **Peroniceratidae**. Similar to *Mammitidae* in general aspect and ornamentation of adult stage, but young have a distinct keel and a coronate form with heavy tubercles. Costae generally dichotomous, and venter often has channels or smooth zones on either side of the keel. Sutural outlines more complex than in *Mammitidae*.

Peroniceras, *Gauthiericeras*, Gross.; *Hystrichoceras*, gen. nov. (Fig. 1233). Type *H.* (*Amm.*) *Coupei*, Brongt. sp.; *Dipoloceras*, gen. nov. (Fig. 1234). Type *D.* (*Amm.*) *cristatum*, d'Orb. sp. Cretaceous.

Family 36. **Prionotropidae**. Young resemble some forms of *Mammitidae*, but have a crenulated keel at an early stage, which is persistent. Costae usually finer and

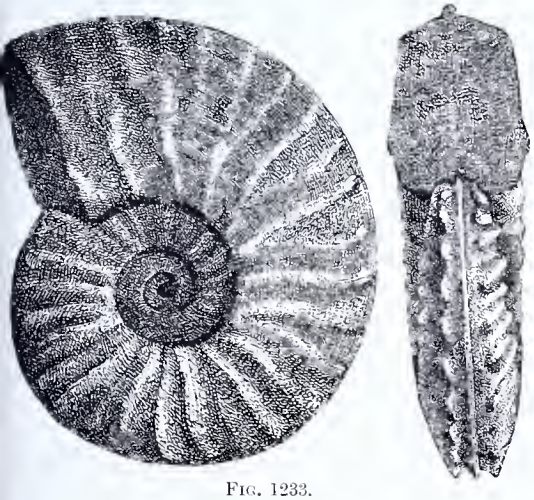


Fig. 1233.

Hystrichoceras varians, Sowb. sp. Cenomanian; Quedlinburg, Saxony.

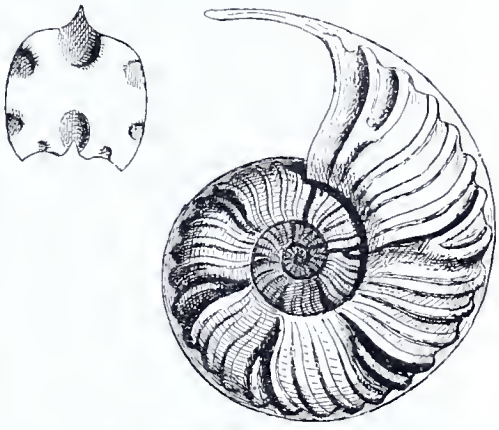


Fig. 1234.

Dipoloceras cristatum, Deluc sp. Lower Cretaceous.

more closely set, and tubercles smaller than in that family. Spines become very large, volutions more quadrate in section, and venter flat with prominent keel and channels until a late stage. Dorsal sutures reduced in discoidal forms to one pair of large saddles and one of incomplete lobes on either side of the antisiphonal.

Prionotropis, *Prionocyclus*, *Mortoniceras*, Meek; *Schloenbachia*, Neum. (Type *S. Germari*, Reuss.). Cretaceous.

Family 37. **Hystatoceratidae.** Similar in general aspect to *Peroniceras*. Young compressed, smooth, and keeled until a late stage; they then become costated, venter loses its keel and is crossed by fold-like costae. Sutures simpler than in preceding families and resemble *Tissotia* except that the first lateral saddles are symmetrically bifid. Dorsal sutures have at least two pairs of zygous saddles and one of zygous lobes; sometimes three pairs of saddles and two of lobes.

Hystatoceras, gen. nov. (*Brancoceras*, Steinm. *non* Hyatt). Type *H.* (*Amm.*) *Senequieri*, d'Orb. sp.; *Hysteroceras*, gen. nov. Type *H.* (*Amm.*) *varicosus*, d'Orb. sp.; *Falloticeras*, Par. and Bon. Cretaceous.

Family 38. **Lenticeratidae.** Young smooth, keeled, discoidal, and resemble preceding family, but adult sutures like those of *Placenticeras*. Saddles very broad and comparatively solid, the first laterals usually with three arms. Arietean lobes not present. Adventitious saddles arise by division and outgrowth of the ventral or outer sides of the first laterals as in *Tissotidae*.

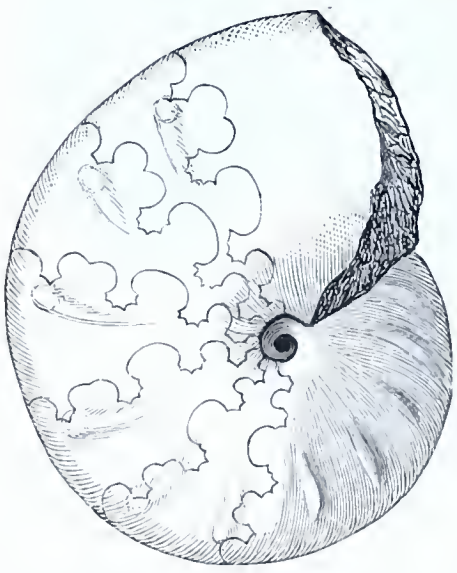


Fig. 1235.

Tissotia Fourneli, Bayle. Cenomanian; Mzab-el-M'saï, Algiers (after Bayle).

Lenticeras, Gerhard; *Paralenticeras*, gen. nov. Type *P.* (*Anal.*) *Sieversi*, Gerhard sp.; *Platylenticeras*, gen. nov. Type *P.* (*Oxynot.*) *heteropleurum*, Neum. and Uhlig sp. Cretaceous.

Family 39. **Tissotidae.** Primitive forms have tuberculated costae and keeled venters, the keel probably having originated by coalescence of a median line of tubercles. Sutures usually very simple, sometimes similar to *Pulchellidae*, and first lateral saddles apt to be unequally bifid. Adventitious saddles appear in some forms, but arise by division of the outer sides of the first laterals instead of from their inner sides as in *Placenticeratidae*.

Tissotia, Douville (Fig. 1235); *Psilotissotia*, gen. nov. Type *P.* (*Pulch.*) *Chalmasi*, Nickles sp.; *Lopholobites*, gen. nov. Type *L.* (*Neol.*) *Cotteaui*, Nickles sp. [*? Hemitissotia*, *Plesiotissotia*, *Heterotissotia*, Peron. Names only reported in *Revue Crit. Pal.* 1899.] Cretaceous.

Incertae sedis: Buchiceras, Hyatt; *Mojsisoricsia*, Steinmann. Cretaceous.

Range and Distribution of the Ammonoidea.

Not less than 5000 species of Ammonoids have been described, as contrasted with about 2500 of *Nautiloidea*. The distribution of these amongst the different sub-orders may be briefly indicated as follows: (1) The *Gastrocampyli* are an aberrant stock confined to narrow limits of the Upper Devonian, and restricted geographically to a few localities in Germany, Russia, and England, with only a single species from the United States.

(2) *Goniatitoids.*—The *Microcampyli* comprise primitive ancestral forms of Ammonoids, and are confined to the Devonian system. The *Mesocampyli* are an aberrant division occurring in both the Devonian and Carboniferous systems, and for the most part enjoy a wide distribution. The most highly specialised family *Pinnacitidae* is limited, however, to only a few European localities. The *Eurycampyli* is by far the most important group of Palaeozoic Ammonoids, and is represented throughout the Devonian and Carboniferous of both hemispheres by typical Goniatitoids. The

Permian and Triassic genera here associated in the same sub-order are parallel with normal Triassic Ceratitoids, and have a wide distribution in the Trias. The *Glossocampyli* is an aberrant stock with peculiar sutures. They begin in the Devonian, but have not yet been traced with certainty in the Carboniferous. They reappear, however, in the Permian, and are represented by a single family in the Trias of India and Northern Siberia. The Devonian and Permian genera are widely distributed.

(3) *Ceratitoids.*—The sub-order *Discocampyli* is restricted to the Trias with the exception of a single family, *Flemingitidae*, which occurs in the Permian of India and North America. The forms have a world-wide distribution, and are especially numerous in India and the western United States. This group attains the acme of specialisation among Ammonoids, as shown by their extremely complex sutures with numerous lobes and saddles, combined with a highly ornamented exterior and considerable modification of form. The number of retrogressive or phylogerontic genera is also very small.

(4) *Ammonitoids.*—The *Phyllocampyli* include the supposed ancestral and primitive forms of typical Ammonoids, and begin with the family *Prolecanitidae*, which ranges from the Devonian to the Permian. Three primitive offshoots of this family are present in the Permian, two of which persist also during the Trias. In all, nine families of *Phyllocampyli* occur in the Trias, only one of which (*Phylloceratidae*) continues throughout the Jura and Cretaceous. Most of the families have a world-wide distribution in the several formations where they occur. The sub-order reaches a high degree of sutural complication, and this, together with the number of lobes and saddles in the *Phylloceratidae*, mark them as being among the most progressive of Ammonoids in respect to sutures. Their shells, however, are very simple in comparison with either the *Discocampyli* or *Pachycampyli*.

The *Leptocampyli* are obviously a retrogressive series. They begin at the base of the Jura with forms having a restricted number of lobes and saddles, and terminate in the Upper Cretaceous with two families of uncoiled phylogerontic shells. The complexity of the sutural outlines is, however, constantly maintained, as is especially well illustrated by *Lytoceratidae*, where the arms of the antisiphonal are curiously prolonged. Their distribution coincides with that of the *Phyllocampyli*, and they are quite abundant in certain Jurassic and Cretaceous localities.

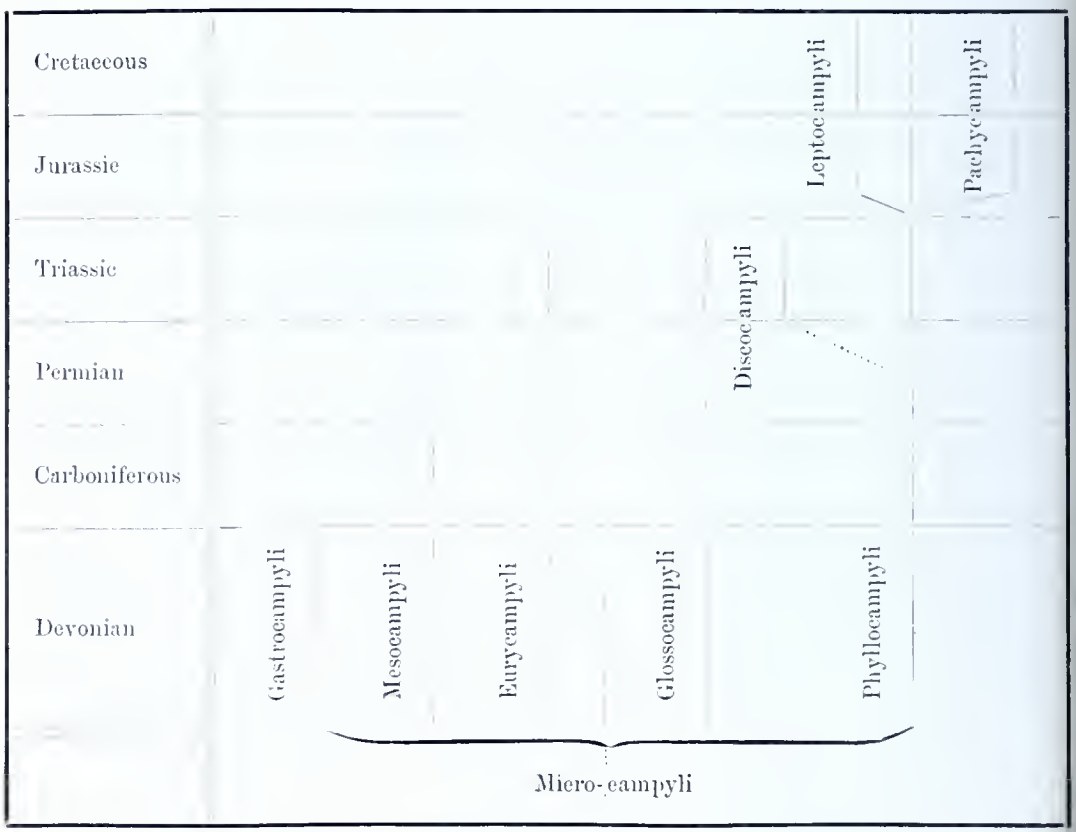
The *Pachycampyli* are usually considered as the typical and also most progressive forms of Ammonoids. This is true as regards the immense number and variety of modifications in form and ornament displayed by their shells and apertures; but the sutural inflections are on the average less complex both in outline and number of lobes and saddles than those of the *Phyllocampyli*, although both groups are evidently derived from the same stock.

By the term *progression*, as used above, is meant "evolution of structures increasing by differentiated additions," such as the addition of more complex inflections to either the dorsal or external sutures, increase in the amount of involution, or the introduction of keels and channels on a primitively convex venter, etc. *Retrogression* signifies "evolution through the reduction of such progressive characters," whether taking place locally or generally in the organism or throughout the group. Retrogression, in this structural sense, does not imply actual reversion to ancestral conditions, except in so far as the disappearance of a part or organ necessarily produces a certain resemblance to their ancestors before the parts or organs in question were evolved. Examples will be found on comparing *Baculites* with *Bactrites*, *Mimoceras* with *Crioceras*, etc. In this sense Ammonoids experienced a progressive evolution from the early Devonian until the Upper Trias, when the first signs of general retrogression are observed, and a few uncoiled and turriliticonic genera appear.

Following their culmination in the Trias, Ammonoids display in the Jura a mixture of retrogressive with some progressive features. Part of their losses are regained by the evolution of a vast number of forms and modifications during this

period, but there are numerous localised signs of retrogression, due perhaps to unfavourable surroundings. Indications of this kind occur sporadically throughout the Jura and become general in the Cretaceous, leading us to infer a widespread unfavourable change in their physical surroundings, similar but more extensive than that which affected European forms during the Inferior Oolite. To the latter influence should probably be ascribed the uncoiling observed in the *Spiroceratidae*. With the close of the Cretaceous all species disappear for ever from the pages of geological history.

TABLE SHOWING RANGE AND PRESUMABLE KINSHIP OF AMMONOID SUB-ORDERS.



[Professor Hyatt's revision of the Nautiloids and Ammonoids for the present work terminates at this point. The classification and diagnoses are condensed from an exhaustive Monograph on fossil Cephalopods, at present still in MS., which embodies the results of his life-study. Reference should be made to this work, when published, for a more complete account of families and genera than it has been possible to give in the preceding pages.—TRANS.]

Sub-Class 2. DIBRANCHIATA.

Cephalopods with only two arborescent gills in the mantle-cavity; provided round the mouth with eight or ten arms bearing suckers or hooks, two of them (when ten in all are present) being often developed into long tentacles. Funnel closed; ink-sac usually present. Shell internal, or if external, is not chambered; in many forms entirely wanting.

The body of Dibranchiates or Cuttle-fishes is elongated, cylindrical, or sack-shaped, and frequently provided with two lateral fin-like appendages. The anterior cephalic region gives off a circlet of eight or ten powerful, muscular arms, the inner sides of which are armed with suckers (*acetabula*), or a double row of hooks, and assist in swimming or creeping, and also serve for the capture of prey. The *Sepioidea* have two of their ten arms developed into very long tentacles which bear hooks or suckers only at their thickened extremities (Fig. 1236). The lower surface of the suckers is disk- or cup-shaped, perforated in the middle, and occupied by numerous radially arranged muscle fibres; they are also occasionally furnished with horny hooks or sharp claws. Each sucker is able to create a partial vacuum by pressing the cartilaginous rim against some object and then contracting the inner folds, and hence can be used like a cupping-glass.

The jaws resemble those of Nautiloids in form, but are never calcified; owing to their perishable nature, usually horny, they are not preserved in the fossil state. The cartilage of the head forms a complete ring enclosing the central portion of the nervous system. The eyes are of a large size, protected by a capsule, and recall those of vertebrates in structure.

The body is constricted at the mantle opening, which occurs just behind the head, and at this point on the ventral surface is placed the respiratory orifice, bounded by a projecting fold of the mantle. Here also terminates the cylindrical or conical funnel, on either side of which lie the dendriform gills; in the same neighbourhood too are placed the anal and genital openings.

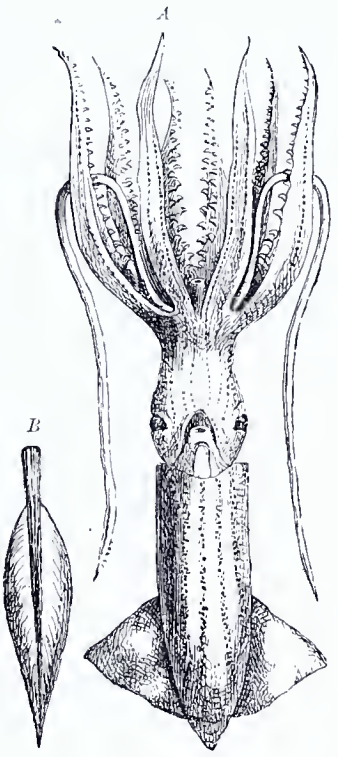


Fig. 1236.

Enoploteuthis leptura. Recent; Pacific Ocean. *A*, Ventral aspect. *B*, Internal shell.

The abdomen is sack-shaped, and contains besides the viscera and circulatory systems a rather large pyriform vessel called the ink-bag. Its reservoir is filled with an extremely opaque brownish-black fluid, which can be voided at will through an excurrent canal terminating near the anus. Menaced or alarmed, the creature discharges an impenetrable cloud of ink, which serves to conceal its retreat. One often finds within the body of fossil Dibranchiates not only a cast or mould representing the ink-bag, but often a dark-coloured residuum of the carbonaceous particles suspended in the ink.

The abdomen is completely covered by the mantle, which is a thick and frequently brilliantly coloured muscular envelope. Traces of it are occasionally found among fossil forms, owing to a slight secretion of calcareous matter within it.

Most Dibranchiates secrete an internal shell within the mantle. Only among the *Octopoda* is a shell absent entirely, or replaced in the female by a thin, simple, unchambered spiral; but this last is in nowise homologous with the usual Dibranchiate shell. *Spirula* has a spiral, camerated shell, the septa of which are traversed by a siphuncle, and whose coils are not in contact. It

is situated in the hinder portion of the body and is partially enveloped by the mantle. Among extinct *Belemnites* the internal shell consists of three parts: a chambered cone (*phragmocone*), which is prolonged forwards on the dorsal side into a delicate corneo-calcareous *proostracum*, and is inserted at the posterior end into a finger-like calcareous piece called the *guard* (sheath or rostrum), (Fig. 1237, *C*).

Some living Cuttle-fishes have an elongated-oval, horny, feather-shaped proostracum or "pen" (Fig. 1255), which is situated dorsally in a closed sac of the mantle. It is sometimes extremely thin, and composed of conchyolin or lime carbonate. The gladius or "cuttle-bone," as the shell is called when calcified in some genera, retains a vestige of chambering at its posterior end, but as a rule exhibits no indication of a phragmocone, properly speaking.

Many living Dibranchiates are gregarious, and swim in the open sea in hordes; others creep on the bottom or lead a separate existence along rocky shores. They are extraordinarily active, voracious animals, and prey upon mollusks, crustaceans, and fishes. A few species are esteemed as food by man. In size Dibranchiates are extremely variable; some forms are only 2 or 3 cm. long, and others attain gigantic dimensions. *Architeuthis*, for example, reaches a total length of 12 metres, the body being 2·5 long, and over 2 metres in circumference. Its arms are thick as a man's leg, and the suckers sometimes as large as ordinary coffee-cups.

Dibranchiates are divided into three sub-orders, as follows:—*Belemnoidea*, *Sepioidea*, and *Octopoda*.

Sub-Order A. **BELEMNOIDEA**. (*Phragmophora*, Fischer.)[1]

Shell internal, chambered, and the septa traversed by a siphuncle; conical or more rarely spiral, and (with the exception of Spirula) terminating posteriorly in a calcareous sheath or guard. Arms ten in number, provided with hooklets. Trias to Recent.

Save for the genus *Spirula*, all forms belonging to this sub-order are extinct. Their camerate shells, perforated by a siphuncle, betoken a kinship with Tetrabranchiates, but there are decided differences both in shell-structure and function. Tetrabranchiates have the shell always external, enclosing the body, but in the present group it is enveloped by the soft parts. Direct connection between the *Sepioidea* and *Belemnoidea* is apparent, and although their shells differ in form and structure, yet a rudimentary phragmocone persists in the former at the posterior end of the skeleton. This rudiment is much more perfectly developed in *Belosepia* of the Tertiary, which is a connecting-link between Belemnoidea and Sepioidea. It is possible to explain the entire internal shell of *Spirula* as homologous with the phragmocone of *Belemnites*. It begins as a globular or inflated protoconch, which is constricted off from the first camera, and is devoid of a cicatrix. The siphuncle originates as a caecal tube, and is continued apicad as a prosiphon, the same as in Tetrabranchiates.

Family 1. **Belemnitidae**. de Blainville.

Shell composed of a conical camerate phragmocone, continued on the dorsal side as a proostracum, and an elongated solid rostrum or guard. Arms ten in number, of equal length, provided with hooklets. Ink-bag present. Trias to Eocene.

[1] In addition to the principal literature, cited on pp. 502-505, see the following:—*Crick, G. C.*, On Coccoteuthis and Acanthoteuthis (Geol. Mag. [4], vol. III. (1896), p. 439, and IV. (1897), p. 1).—*Huxley, T. H.*, and *Pelseneer, P.*, Report on Spirula (Appendix Challenger Rep., Zoology, Part LXXXIII.), 1895.

This family, owing to its great diversity of forms and geological importance, occupies a foremost position among *Belemnoidea*. The shell may be considered as the prototype of that in all Dibranchiates, since it has all the component parts fully developed, whereas in other groups some of these become atrophied.

The shell of *Belemnites* (Fig. 1237) consists of three fundamental portions: (1) A solid calcareous piece, usually much elongated, and of sub-cylindrical, conoidal, or fusiform shape. This is called the *guard* (*rostrum*, *osselet*, *gaine*, *Scheide*), and is excavated at its anterior broad extremity into a conical cavity or alveolus. Within the alveolus is placed (2) the *phragmocone*. This consists of a conical series of chambers (loculi), the septa of which are pierced at the ventral margin for the passage of the siphuncle. The phragmocone begins with a globular protoconch, and its last or anterior chamber is of comparatively large size. It is invested with a thin proper wall (conotheca), which is prolonged forwards on the dorsal side into a more or less calcified plate called (3) the *proostraeum*. This last corresponds to the "pen" of living cuttle-fishes. There is evidence that its anterior margin is convex, but it is so extremely thin that it is never perfectly preserved, and like the phragmocone, is wanting in by far the greater number of specimens.

Notwithstanding the fragmentary condition in which the proostracum invariably occurs, it is possible to reconstruct its outlines from the peculiar *conotheeal striae*, or markings of the membranous substance with which it is invested. The conotheca is made up of three very thin superimposed laminae, the outermost of which usually shows the markings alluded to most distinctly (Fig. 1237, *C*). The conical surface of the phragmocone and proostracum is divided by Voltz into four principal regions radiating from the apex: A dorsal area, including all the space between two straight lines called the *asymptotes*, which extend from the apex of the cone as far as the aperture. This area occupies about one-fourth of the circumference, and is marked with loop lines of growth convex toward the front. On either side of the dorsal area and separated from it by the asymptotes is a lateral or *hyperbolic area*, each one occupying about one-eighth of the circumference, and covered with very obliquely arched lines in a hyperbolic form. The ventral area is covered with numerous transverse striae, of which there are many on each alveolar chamber, and they are closer together the nearer they are to the apex of the phragmocone. The striae of the dorsal area are less numerous than those of the rest of the shell, and usually less pronounced, being sometimes imperceptible.

"The guard of *Belemnites* consists of prismatic calcareous fibres, which are directed perpendicularly to the surface, and radiate in all directions from an axial line, which is not strictly central, but is somewhat nearer the ventral than the dorsal side. The growth of the guard is effected by the deposition of successive conical layers or sheaths, which are secreted over the entire surface, but are thickest behind, and become gradually attenuated in front. The surface of the guard is smooth; or may be wholly or partially granulated or wrinkled; or, again, may be marked with branched vascular impressions, which are especially conspicuous on the ventral side. In many cases a well-marked groove—the ventral furrow—runs from the edge of the alveolus backwards on the ventral side, extending for a short distance only, or reaching to the point of the guard (Fig. 1241, *C*). The apical portion of the guard often shows two symmetrical grooves (the dorso-lateral grooves) which diverge slightly and become shallower as they extend forwards, and which mark the dorsal side of the shell" (Nicholson).

As shown by vascular impressions on the rostrum, the shell of Belemnoids was completely enveloped by the mantle. Natural casts of the animal occurring in the English Lias (Figs. 1237 *B*, 1250) exhibit an elongated form of body, contracted anteriorly, with a small head surrounded by ten equal arms. An ink-sac is present, and the arms are provided with hooks. The maximum size attained by Belemnitoids is between 2 and 2·5 metres.

Aulacoceras, Hauer (Fig. 1238). Guard elongated, clavate, contracted anteriorly, thickened in the posterior third, and pointed at the tip; composed of concentric, loosely superimposed lamellae. Each side marked by a deep broad lateral groove reaching from the tip as far as the anterior alveolar margin. Phragmocone at least twice as long as the rostrum, slowly increasing in width anteriorly, ornamented externally with raised longitudinal lines, which are crossed on the dorsal side by a transverse series, convex toward the front; closely resembling *Orthoceras*. Septa rather distantly spaced; siphuncle marginal, thin; proostracum unknown. Guards of this genus are rare, but detached phragmocones not uncommon. Upper Alpine Trias.

Atractites, Gumb. Like *Aulacoceras*, but guard large, smooth, and without lateral furrows. Phragmocone either smooth, or with fine asymptotic lines, and dorsal area marked with extremely fine growth-lines, convex toward the front. Guards and

phragmocones almost always occur detached. The former originally mistaken for Orthoceratites, but are distinguished by their marginal siphuncle and characteristic conothecal striae. [Hyatt regards both *Aulacoceras* and *Atractites* as descended from Orthoceratites.] Upper Trias and Lias of the Alps.

Xiphoteuthis, Huxley. Lower Lias; England.

Belemnites, Lister (Figs. 1237-1242). Name first applied by Agricola in 1546. Guard dactyliform, subcylindrical, or conoidal, sometimes short and thick, sometimes

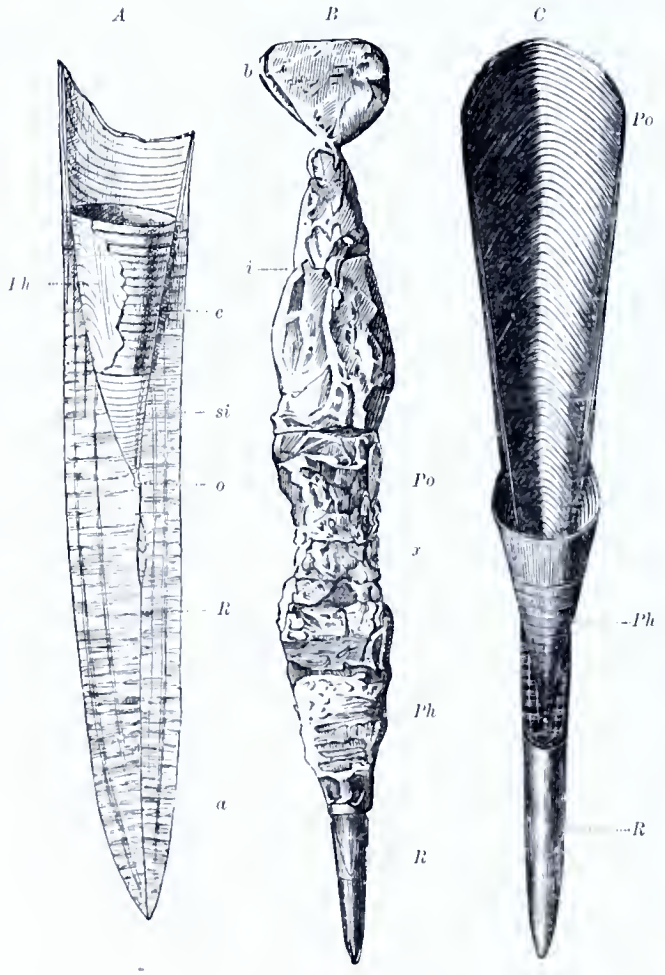


Fig. 1237.

A, Vertical section of a Belemnite, the proostracum broken away above the phragmocone. *B*, *Belemnites Brugierianus*, Miller. Lower Lias; Charmouth, England. Cast of complete individual. 1/3 (after Huxley). *C*, Restoration of a Belemnite shell.

Abbreviations: *R*, Rostrum or "guard"; *Ph*, Phragmocone; *Po*, Proostracum; *a*, Apical line reaching from apex of guard to bottom of alveolus (*o*); *b*, Impression of arms; *c*, Camerae of phragmocone; *i*, Anterior end of proostracum; *o*, Protoconch; *si*, Siphuncle; *x*, Ink-bag.

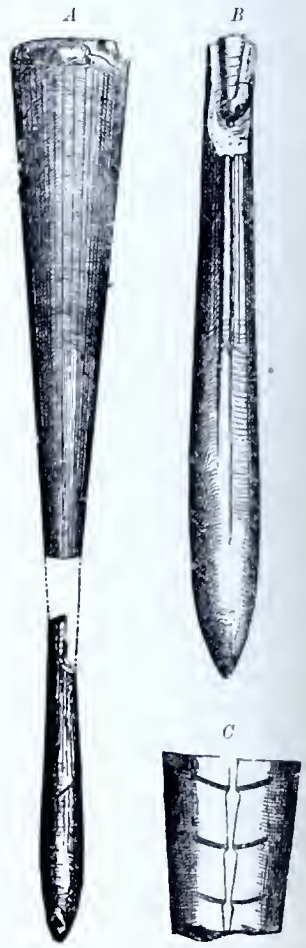


Fig. 1238.

Aulacoceras reticulatum, Hauer. Upper Trias; Röthelstein, near Aussee, Austria. *A*, Guard and phragmocone, 2/3. *B*, Guard, 1/1. *C*, Portion of phragmocone sliced to show siphuncle and siphonal funnels.

slender and much elongated; retral portion tapering, submucronate, or obtusely rounded. Owing to irregularity in secretion of calcite layers on the periphery of the guard during growth, individuals belonging to the same species but of different ages are apt to vary considerably in form. Such differences are well illustrated in *B. acuarius*, Schloth. The young are sometimes fusiform, but grow cylindrical or conical with age. About 350 species are known, ranging from the Lower Lias to summit of the Cretaceous; maximum from Middle Lias to Lower Cretaceous.

Distribution world-wide; most abundant in Europe, Asia, and North America. As an index fossil of the Jura and Cretaceous, this genus is scarcely less important than Ammonites.

Sub-Genera: *Pachyteuthis*, Bayle (Fig. 1241, *A*). Guard perfectly smooth. Confined to Lower Lias. *B. acutus*, Mill.

Megateuthis, Bayle (*Dactyloteuthis*, Bayle; *Paxillosi*), (Fig. 1241, *B*). Apex of guard with two or three usually short grooves. Middle Lias to Lower Cretaceous. *B. paxillosus*, *B. giganteus*, Schloth.; *B. elongatus*, Mill.; *B. subquadratus*, Roem., etc.

Belemnopsis, Bayle (*Hibolithes*, Montf.; *Gastrocoeli*, *Canaliculati*, *Hastati*), (Fig. 1241, *D*, *E*). Guard with deep and usually long ventral furrow extending from alveolar margin toward the apex, with or without dorso-lateral lines. Middle Jura to Middle Cretaceous. *B. canaliculatus*, Schloth.; *B. absolutus*, Fisch.; *B. unicanaliculatus*, Ziet.; *B. minimus*, Lister.

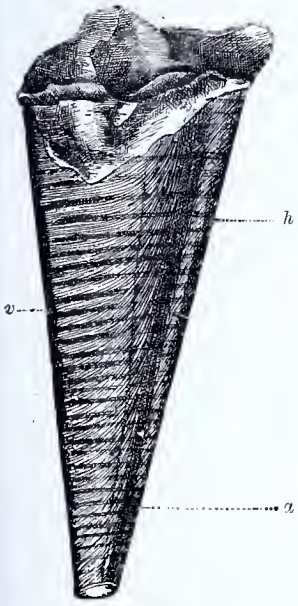


Fig. 1239.

Belemnites compressus. Lias; Gundershofen, Alsace. Phragmocone with well-preserved conotheca. *a*, Asymptotic line; *h*, Hyperbolic area; *v*, Ventral area.

Fig. 1240.

Belemnites (*Duvalia*) *dilatatus*, Blv. Neocomian; Justithal, Lake of Thun, Switzerland.

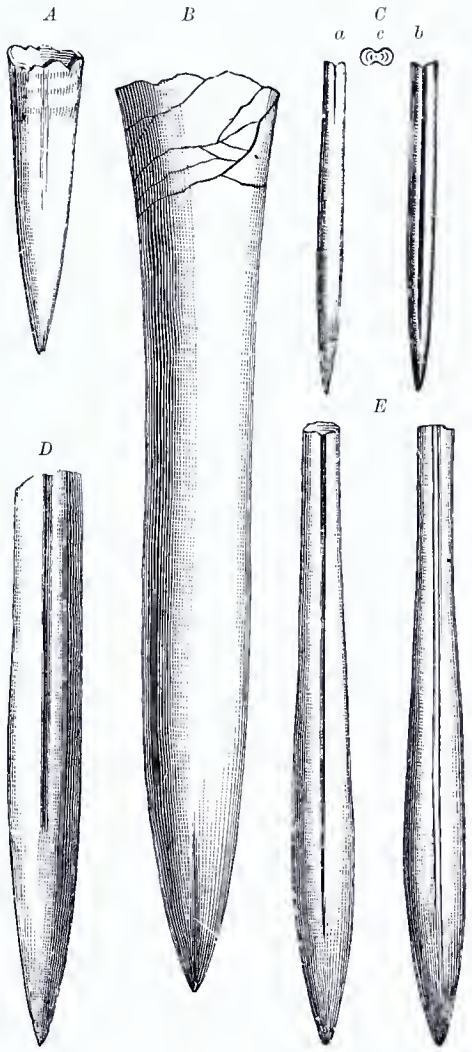


Fig. 1241.

A, *B*. (*Pachyteuthis*) *acutus*, Miller. Lower Lias; Lyme Regis, Dorsetshire. *B*, *B*. (*Megateuthis*) *paxillosus*, Schloth. Middle Lias; Metzingen, Würtemberg. *C*, *B*. (*Pseudobelus*) *bipartitus*, Blv. Lower Cretaceous; Castellane, Basses Alpes. *a*, *b*, *c*, Dorsal and ventral aspects and cross-section, $^1/_1$. *D*, *B*. (*Belemnopsis*) *canaliculatus*, Schloth. Inferior Oolite; Würtemberg. *E*, *B*. (*Belemnopsis*) *hastatus*, Blv. Oxfordian; Dives, Calvados.

Pseudobelus, Montf. (*Bipartiti*), (Fig. 1241, *C*). Guard thin, slender, with deep dorso-lateral grooves, with or without ventral furrows. Upper Lias to Lower Cretaceous. *B. exilis*, d'Orb.; *B. bipartitus*, Blainv.

Actinocamax, Mill. (*Gonioteuthis*, Bayle), (Fig. 1242). Guard cylindrical, submucronate, with short but very deep ventral furrow; anterior end foliaceous, and very liable to dissolution. Phragmocone only very slightly inserted in the guard, the two portions usually separated by an interval. Middle and Upper Cretaceous. *B. subventricosus*, Wahlb.; *B. quadratus*, Blainv.

Belemnitella, d'Orb. (Fig. 1243). Guard cylindrical, with short, deep ventral furrow falling short of alveolar margin. Phragmocone inserted in guard. Vascular impressions often beautifully preserved. Upper Cretaceous.

Diploconus, Zitt. (Fig. 1244). Guard short, obtusely conical, and having a concentric lamellar structure, not radial and fibrous. Phragmocone reaching nearly to posterior end of guard. Tithonian.

Bayanoteuthis, Mun.-Chalm. Guard long, cylindrical, mucronate, with shallow lateral grooves. Dorsal area roughened. Phragmocone very slender and long, oval in section. Eocene. *B. rugifer*, Schloenb.

Vasseuria, Mun.-Chalm. Guard slender, elongated-conical, with three longitudinal grooves extending from the apex. Alveolus over half as long as the guard.

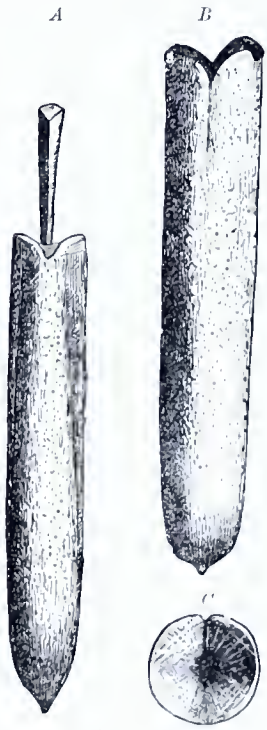


Fig. 1242.

Belemnites (*Actinocamax*) *quadratus*, Blv. sp. Upper Cretaceous; Germany. *A*, Dorsal view of guard with deformed phragmocone projecting from alveolus. *B*, Ventral aspect of guard. *C*, Alveolus from above (after Schlüter).

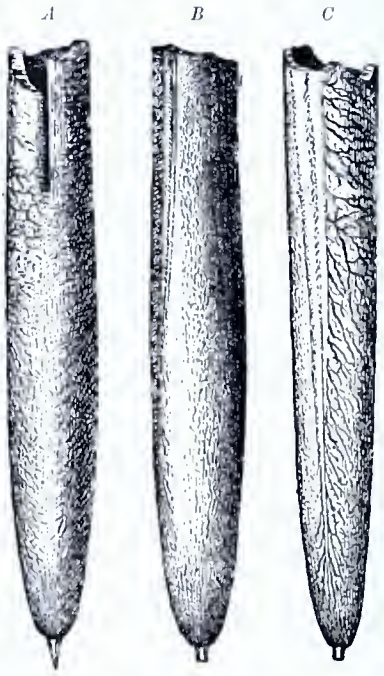


Fig. 1243.

Belemnites (*Belemnitella*) *mucronatus*, Schloth. Upper Cretaceous; Drensteinfurth, Westphalia. *A*, *B*, *C*, Ventral, dorsal, and lateral aspects. 2/3.

Fig. 1244.

Diploconus belemnitoidea, Zittel. Tithonian; Stramberg.

Fig. 1245.

Beloptera belemnitoidea, Blv. Calcaire Grossier; Paris Basin. Ventral aspect.

Siphonal funnels extending from one septum to the next. Very rare in Eocene of Pretagne.

Belemnosis, M. Edw. Very rare in English Eocene.

Beloptera, Blainv. (Fig. 1245). Guard short, composed of two cones placed with their apices against one another and united by a central expansion which projects outwardly on either side. Anterior cone with alveolus. Phragmocone unknown. Eocene.

Belopterina, Mun.-Chalm. Like *Beloptera*, but without the lateral wing-like expansions. Eocene.

Family 2. **Belemnoteuthidae.** Zittel.

Shell composed of a conical phragmocone and proostracum, the rostrum being reduced to a thin calcareous investment of the phragmocone. Ten arms of nearly equal length, each beset with a double row of hooks. Ink-sac present. Trias and Jura.

Acanthoteuthis, Wagner and Münst. (*Belemnites*, Quenst. p.p.; *Ostracoteuthis*,

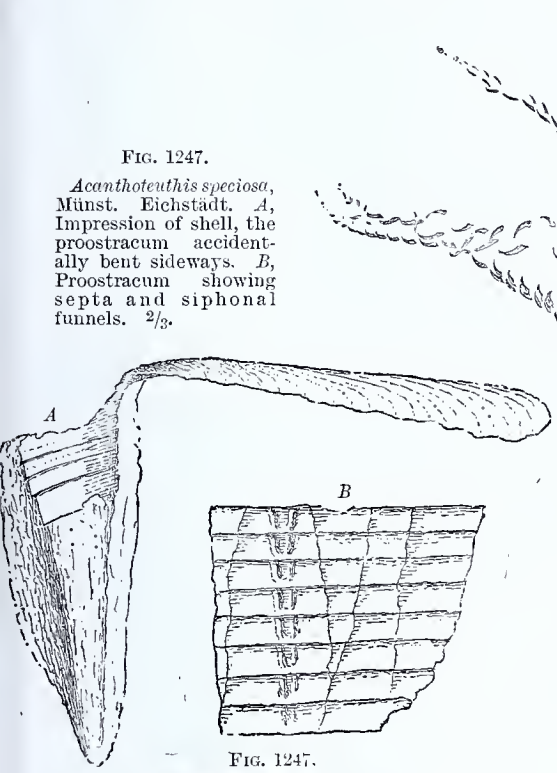


Fig. 1247.

Acanthoteuthis speciosa, Münst. Eichstädt. *A*, Impression of shell, the proostracum accidentally bent sideways. *B*, Proostracum showing septa and siphonal funnels. 2/3.

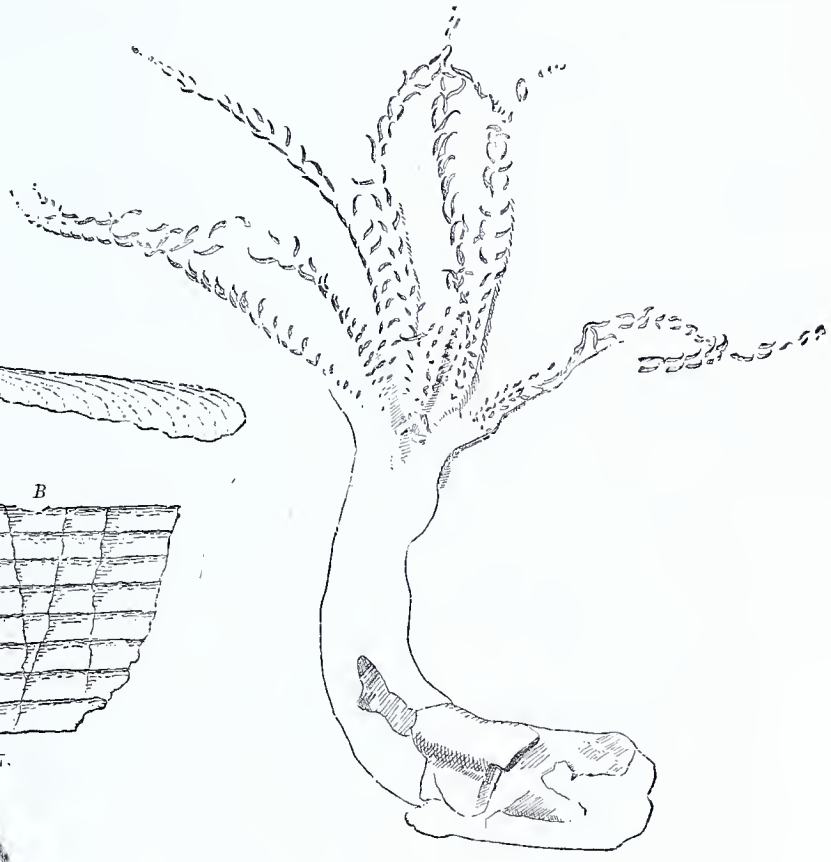


Fig. 1246.

Acanthoteuthis speciosa, Münst. Lithographic Slates; Eichstädt, Bavaria. Impression of arms and body. 1/2.

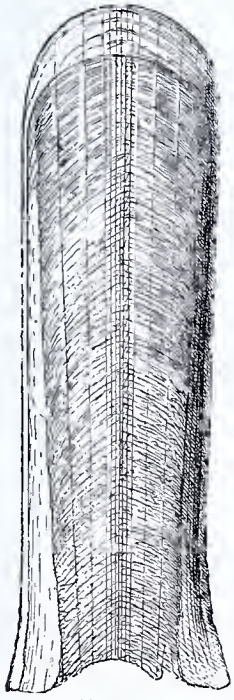


Fig. 1248.

Acanthoteuthis speciosa, Münst. Solenhofen. Proostracum. 2/3.

Zitt.), (Figs. 1246-1248). Phragmocone with numerous septa, and siphuncle having short siphonal funnels; enveloped externally in a thin granular calcareous layer representing the guard. Surface of proostracum divisible into a broad dorsal, and two narrow lateral areas which are longitudinally striated and taper toward the front. Dorsal area ornamented with fine parabolic and also straight longitudinal lines; anterior margin rounded. An impression of the animal found in the Lithographic Slates shows an ink-bag and ten powerful arms about the head, which are beset with two rows of opposite, horny, falciform hooklets. Upper Jura.

Phragmoteuthis, Mojs. (Fig. 1249). Proostracum twice as long as the conical phragmocone, with dorsal area bounded by asymptotic lines, and two shorter lateral areas; anterior margin of all areas rounded. Phragmocone invested by a brownish layer representing the guard. Trias (Raibl Beds).

Belemnoteuthis, Pearce (*Conoteuthis*, d'Orb.), (Figs.

1250, 1251). Like *Acanthoteuthis* but smaller, and phragmocone not produced into a long proostracum. Upper Callovian and Lower Cretaceous.

Fig. 1249.

A, *Phragmoteuthis bisinuata*, Bronn. sp. Trias; Raibl, Carinthia. *Ph*, Phragmocone; *Po*, Proostracum; *L*, Lateral area of proostracum; *d*, Ink-bag. *B*, Hooklets of arms, 1/1 (after Suess).

Fig. 1250.

Belemnoteuthis antiqua, Pearce. Oxford Clay; Christian Malford, Wilts. *A*, Partly restored specimen, 1/2. *oc*, Eyes; *m*, Mantle. Other letters as in Fig. 1249. *B*, Hooklet, 4/1 (after Mantell).

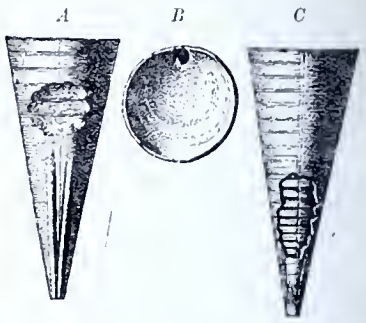


Fig. 1251.

Belemnoteuthis, Pearce sp. Oxford Clay; Gammelshausen, Würtemberg. *A*, *C*, Dorsal and ventral aspects. *B*, Septum and siphuncle.

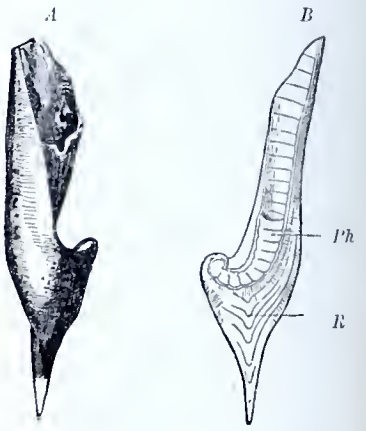


Fig. 1252.

Spirulirostra Bellardii, Mich. sp. Miocene; Superga, near Turin, Italy. *A*, Side view. *B*, Longitudinal section. *R*, Guard; *Ph*, Phragmocone. 1/1 (after Munier-Chalmas).

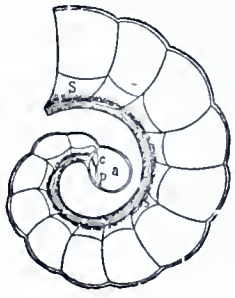


Fig. 1253.

Spirula Peronii, Lam. Recent; Pacific. Longitudinal section, 1/1. *a*, Protoconch; *c*, Caecal commencement of siphuncle; *p*, Prosiphon; *s*, Siphuncle after Munier-Chalmas).

Family 3. **Spirulidae.** Zittel.

Shell reduced to a chambered phragmocone coiled into a flat spiral, the coils not in contact; situated in posterior part of the body, and the greater portion contained within the mantle. In addition to the eight arms, two long tentacles without hooks are placed between the third and fourth pairs. Pliocene and Recent.

Spirulirostra, d'Orb. (Fig. 1252). Shell composed of a short triangular pointed guard, which is excavated anteriorly for the reception of the chambered phragmocone. The latter begins as a spiral, but speedily becomes straight, and has septa pierced on the concave ventral side by the marginal siphuncle. Only one species. Upper Miocene of Turiu.

Spirulirostrina, Canavari. Like the preceding, but guard reduced to two small, lateral wing-like appendages. Neocene of Sardinia.

Spirula, Lam. (Fig. 1253). Guard wanting. Chambered phragmocone enrolled

with the ventral side concave, the coils not in contact, composed of nacreous substance; septa concave; protoconch globular. Siphuncle ventral and marginal in position, completed by siphonal funnels extending between the septa. Prosiphon present. Recent; inhabits tropical seas. [For description of the animal see "Zoology," Part LXXXIII., of *Challenger Reports*, 1895.]

Sub-Order B. SEPIOIDEA. Cuttle-fishes.

Shell internal, without differentiated phragmocone and guard, but consisting essentially of proostracum or "pen," which is either oval, or narrow and elongated. Arms ten in number, provided with suckers or hooks. Ink-bag present.

Family 1. Sepiophoridae. Fischer.

Skeleton calcareous, elongated-oval, terminating posteriorly in a thickened mucro which represents a rudimentary phragmocone and rostrum, and encloses a conical cavity. Siphuncle wanting.

The thickened posterior mucro is a rudimentary structure probably corresponding to the guard of Belemnoids, and its conical cavity to the alveolus *Belosepia* retains a vestigial chambering but no siphuncle, and in *Sepia* a recognisable phragmocone is wholly wanting.

Belosepia, Voltz (Fig. 1254). As a rule only the posterior portion of the proostracum is preserved. This ends in a bent spine, which is thickened anteriorly, laterally expanded, and contains near the apex a conical alveolus. The latter shows on the dorsal side incomplete traces of septa, and a wide funnel-like depression occupies the place of a siphuncle. Eocene; not uncommon in Paris Basin.

Sepia, Lam. (Fig. 1255). Proostracum of equal length with the mantle, elongated-oval, rounded anteriorly, thickened posteriorly and terminating in a short mucro. The latter contains a conical alveolus. External walls of proostracum consisting of two brittle calcareous laminae, separated by a horny layer. Internally with a mass of extremely fine parallel calcareous lamellae, increasing in thickness anteriorly; the lamellae separated from one another by minute vertical rods, thus producing a spongy texture. The familiar cuttle-bone of commerce or *ossa Sepiae*, is the pen of *Sepia officinalis*, Linn., and is found in great quantities along the coast of certain countries. Several Tertiary species known.

Fig. 1254.

Belosepia Blainvillei, Desh. Eocene; Auvers, near Paris. *A*, Posterior end of shell, ventral aspect. *B*, Same from the side (after Deshayes).

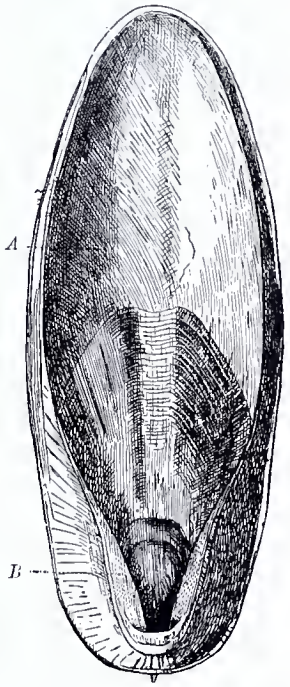


Fig. 1255.

Sepia officinalis, Linn. Recent. Ventral view of shell. *A*, Calcareous lamellae of proostracum. *B*, Position of rudimentary phragmocone in front of mucro, 2/3.

Family 2. **Chondrophoridae.** Fischer.

Proostracum much elongated, thin, composed of conchiolin or of alternating layers of calcareous and horny matter, thickened posteriorly, and without conical alveolar cavity. Jura to Recent.

Coccoteuthis, Owen (*Trachyteuthis*, v. Meyer (Fig. 1256). Proostracum elongated-oval, composed of calcareous and horny laminae, rounded posteriorly or with but slightly projecting mucro; external surface roughly granulated, and marked by lines diverging from the apex. These lines limit the boundaries of two wing-like expansions projecting from the sides of the elongated median portion. Impressions of the body and arms occasionally found in the Lithographic Slates of Bavaria. Upper Jura.

Leptoteuthis, v. Meyer. Proostracum very large, thin, narrowing posteriorly, and composed of several layers of calcareous and horny layers. Median area ornamented

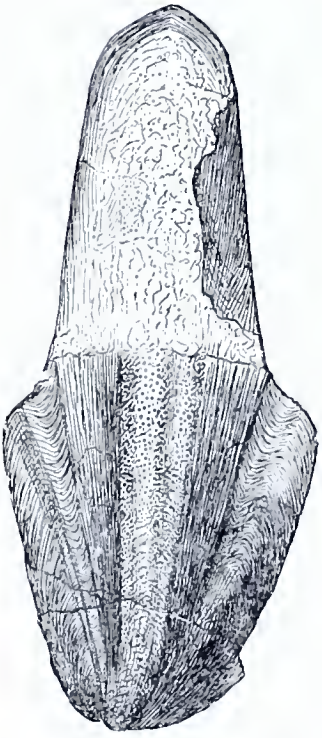


Fig. 1256.

Coccoteuthis hastiformis, Rüpp. sp. Lithographic Slates; Eichstädt, Bavaria.

Fig. 1257.

Belotenthis Schuehleri, Quenst. Upper Lias; Holzmaden, Würtemberg. 1/2 (after Quenstedt).

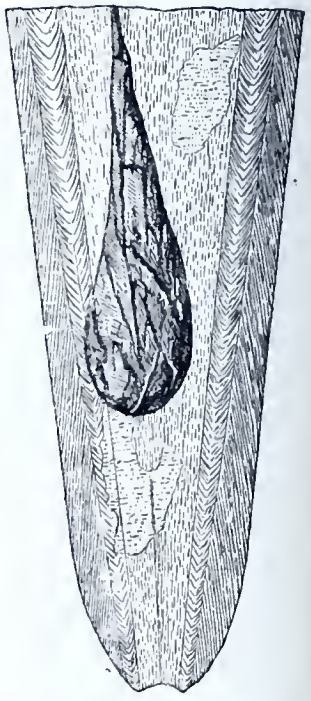


Fig. 1258.

Geoteuthis Bollensis, Zieten. Upper Lias; Holzmaden, Würtemberg. Shows ink-bag and conothecal striae. 1/3.

with fine undulating transverse striae, convex toward the front, and separated from the lateral areas by longitudinal lines diverging from the apex. Lateral areas marked with oblique inwardly directed lines, and bordered by lateral expansions which are widest posteriorly. Upper Jura of Southern Germany. *L. gigas*, v. Meyer.

Geoteuthis, Münst. (Fig. 1258). Proostracum composed of thin alternating horny and calcareous layers, widest in front, rounded posteriorly. Median area divided into halves by a longitudinal line, and bounded on either side by lateral areas with hyperbolic striae. Ink-bag frequently preserved, the contents transformed into a jet-like substance. It is possible to dissolve the carbonaceous particles so as to prepare a wash resembling India ink. Upper Lias of Germany, France, and England.

Belotenthis, Münst. (Fig. 1257). Proostracum very thin, elongated, feather-shaped,

broadly rounded posteriorly, pointed in front, traversed by a median longitudinal keel. Upper Lias of Würtemberg.

Teuthopsis, Desl. Lias. *Celaeno*, Münst. Upper Jura. *Phylloteuthis*, Meek and Hayden; *Actinoscpia*, Whiteaves. Cretaceous.

Plesioteuthis, Wagner (Fig. 1259). Proostracum very thin, long, narrow, lanceolate, pointed posteriorly, rounded in front, with a median longitudinal keel and a raised line along each of the lateral edges. Very abundant in Lithographic Slates, and impressions of the body and head not uncommon. Also found in Cretaceous of Maestricht and Syria.

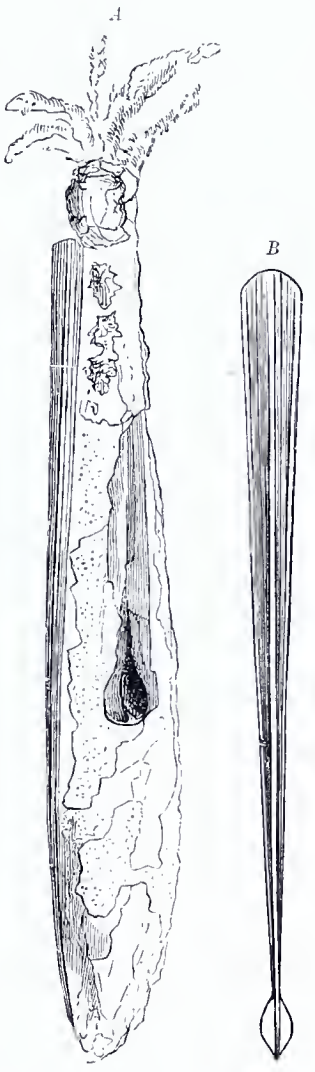


FIG. 1259.

Plesioteuthis prisca, Rüpp. sp. Lithographic Slates; Eichstädt. *A*, Impression of animal showing arms and ink-bag. *B*, Shell, 1/2.

Sub-Order C. OCTOPODA.

Body without internal shell, and only the female of Argonauta secreting a single-chambered external shell. The two tentacles are not present, and the eight arms bear sessile suckers without horny rims. Eye relatively small, without sphincter-like lid. Body short and rounded, usually without fin-like appendages.

The majority of genera belonging here are naked and therefore without fossil representatives. The small male of *Argonauta*, Linn., is without a shell, but the large female bears a delicate, boat-shaped, spiral shell which is secreted partly by the mantle, and partly by two fin-like expansions of the dorsal arms. Outer surface of shell ornamented by folds and tubercles, and two nodose ventral keels are present. Late Tertiary and Recent.

Vertical Range of the Dibranchiata.

As compared with Tetrabranchiates, the *Dibranchiata* are of subordinate geological importance. Their entire organisation renders them less well adapted for preservation in the fossil state, and accordingly we shall never be able to form even an approximate idea of their importance in their contemporaneous faunae. The earliest representative of *Belemnoidea* appears in the Trias (*Aulacoceras*), and the *Sepioidea* are initiated in the Lias. From what group Dibranchiates are descended, whether from the Tetrabranchiates or from primitive naked ancestors, we have at present no certain means for determining. They appear suddenly in a high state of development; but a still more remarkable fact is the swift culmination and decline of the group of Belemnoids. In place of the small number of forms met with in the Trias, we find even in the Lias, as well as other divisions of the Jura and Lower Cretaceous, a rich and varied Belemnite fauna. At the close of the Cretaceous only two genera, *Belemnitella* and *Actinocamax*, persist in relatively large numbers, and although a few antiquated relics of the same stock hold over into the Eocene, their very rarity demonstrates waning vitality. The sole living representative of Belemnoids is the genus *Spirula*.

In all probability the *Sepioidea* are descended from Belemnoids. *Belosepia* of the Tertiary has tolerably distinct indications of a phragmocone, but in *Sepia* proper this

structure is reduced to the merest rudiment. Jurassic *Chondrophoridae* approximate closely to recent members of the same family. All the evidence at our disposal justifies the conclusion that Mesozoic Cuttle-fishes possessed an essentially similar organisation to that of recent forms.

[The rendering into English of the original text for the chapters on *Mollusca*, exclusive only of the Dibranchiates (*Grundzüge*, pp. 250-435), was performed by Dr. John C. Merriam, Professor of Palaeontology in the University of California. His careful translation greatly facilitated the labours of Professors Dall, Pilsbry, and Hyatt in their revision of the several groups accredited to them.—TRANS.]

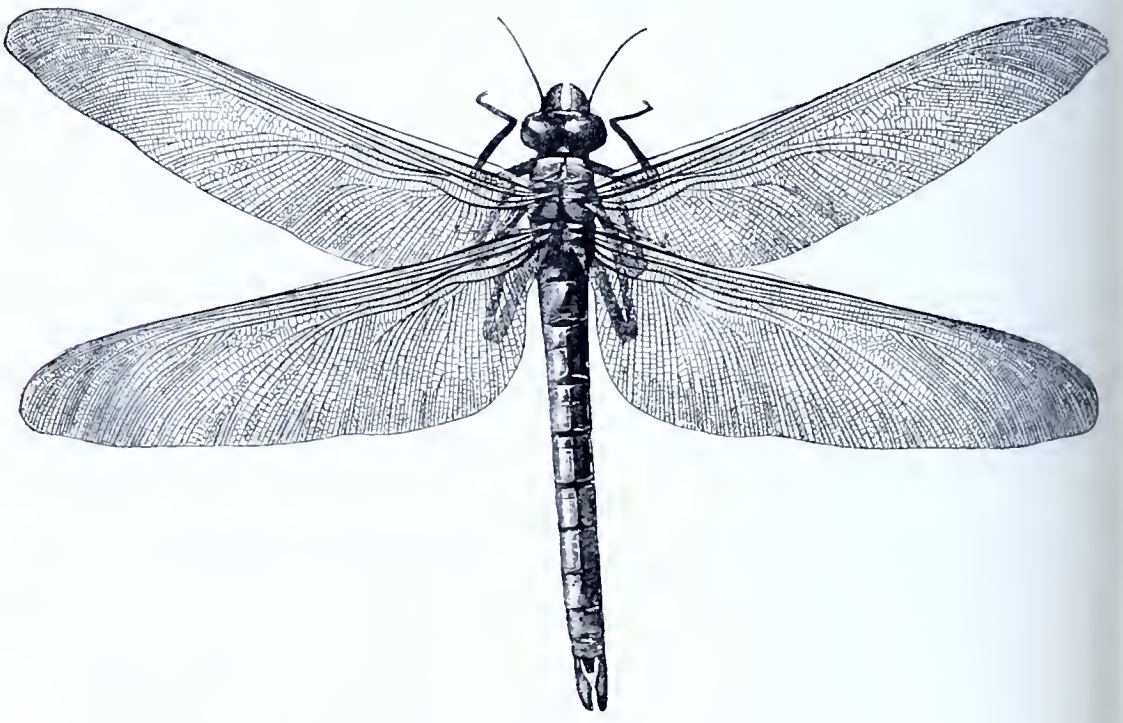


FIG. 1260.

Restoration of *Meganeura Monyi* Brongt. Carboniferous; Commentry. 1/6 natural size (after Charles Brongniart). See page 684.

Sub-Kingdom VII. ARTHROPODA. (Articulates.)

Heteronomously segmented animals with, typically, a pair of appendages to each somite of the body; the whole enclosed in a chitinous segmented exoskeleton, the jointing of which extends to the appendages.

In the *Arthropoda* the segments are unequally developed, and the appendages, primitively locomotor in function, may be modified on one or more somites to subserve special functions, such as the seizure and comminution of food, respiration, sensation, copulation, oviposition, fixation, etc. These modifications of the appendages and the more or less complete union of the segments into groups may result in the differentiation of three distinct regions: head, thorax, and abdomen. Of these regions the head is concerned largely in sensation and feeding, the thorax is chiefly locomotor in function, and the abdomen frequently defensive.

The brain lies above and in front of the oesophagus, and consists of a fusion of several pairs of ganglia. The rest of the central nervous system consists of a chain of ganglia lying in pairs on the ventral surface, with typically a pair in each somite. Not infrequently there is a more or less extensive concentration or fusion of these ventral ganglia. The eyes may be simple, aggregate, or compound, with in some cases an inversion of the retinal layer.

Respiration in the smaller forms is by the general surface of the body, whereas in the larger certain regions become specialised for this purpose. When respiratory outgrowths protrude from the body wall they are known as gills or *branchiae;* when invaginated they are termed *lungs* if they be lamellar in arrangement, or *tracheae* if they consist of fine tubes ramifying through the tissues.

Excretion is effected either by "segmental organs" (true nephridia) which open at the inner end into the true body cavity (*coelom*) and at the other to the exterior, or by diverticula developed at the hinder end of the alimentary canal. The nephridia when present occur in only a few segments of the body. The diverticula of the alimentary canal (Malpighian tubes) are of two kinds—one developed from the mesenteron, the other from the proctoderm. In all Arthropods the ducts of the reproductive organs are apparently modified nephridia, and the organs themselves consist of gonads developed from the coelomic walls. The circulation depends upon a dorsal heart enclosed in a vascular pericardial sac, and metameric blood-vessels terminating in "lacunar" spaces.

Arthropods are divisible into three groups or sub-phyla, distinguished according to the nature of the respiratory organs, segmentation of the body,

and structure of the appendages as follows:—*Branchiata*, *Myriopoda*, and *Insecta*. These are in turn divided into several classes, all of which have fossil representatives. As to the origin of the phylum, Palaeontology affords no certain evidence. The entire organisation of Arthropods indicates a close relationship with *Vermes*, and especially with the group of Annelid Worms; nevertheless, the differentiation of the Arthropod type must have antedated the Cambrian, since several orders of Crustacea are encountered in the oldest fossiliferous rocks which are almost as widely divergent from the supposed ancestral form as many recent forms. The relatively late appearance of Myriopods, which are the most worm-like of all Articulates, may be accounted for by their terrestrial habitat and destructibility of their body parts.

Sub-Phylum A. Branchiata.

Arthropods breathing by means of gills (or lungs or tracheae modified from gills) developed always in connection with the appendages. Head and thorax rarely distinct, but usually more or less completely united in a cephalothorax. The genital ducts open to the exterior near the middle of the body, and true nephridia usually occur. Malpighian tubes, when present, are derived from the mesenteron. Anterior appendages all multiarticulate, the basal joints of one or more pairs serving as organs of manducation.

The branchiate Arthropods include two classes: *Crustacea* and *Acerata*.

Class 1. CRUSTACEA.[1]

Arthropods of usually aquatic habitat, and breathing by gills (exceptionally through the general body surface); with one or two pairs of appendages (antennae) in front of the mouth, the first of which is purely sensory, and several pairs of post-oral appendages, some of which are modified into organs of mastication. Appendages with typically a basal joint (protopodite) giving rise to two or three branches.

The segmentation of the body is distinct in all except certain parasitic forms, where it is lost in the adult stage through degeneration. Usually the demarcation between head and thorax is obscure, and the anterior region of the body consists of a *cephalothorax*, the number of whose segments varies within wide limits; this being in sharp contrast to the *Acerata*, where the segments are constantly six in number. The cephalothorax is frequently covered by a chitinous shell or *carapace*, developed from the dorsal portion of

[1] Literature:

Brongniart, A., and *Demarest, A.-G.*, Histoire naturelle des Crustacés fossiles sous les rapports zoologiques et géologiques. Paris, 1822.

Milne-Edwards, H., Histoire naturelle des Crustacés. 3 vols. Paris, 1834-40.

Woodward, H., and *Salter, J. W.*, Catalogue and Chart of Fossil Crustacea. London, 1865.

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Gerstaecker, A., Crustacea, in vol. V. of Bronn's Classen und Ordnungen des Thierreichs. Part 1 (Cirripedia, Copepoda, Branchiopoda, Poecilopoda, Trilobita), Leipsic, 1866-79; Part 2 (Isopoda to Decapoda), 1881-94.

Vogdes, A. W., A Catalogue of North American Palaeozoic Crustacea confined to the non-trilobitic Genera and Species (Ann. N.Y. Acad. Sci., vol. V.), 1889.

Grobben, K., Genealogy and Classification of the Crustacea (Sitzungsber. Akad. Wissensch. Wien Bd. CI., Heft 2), 1892. Translated in Ann. and Mag. Nat. Hist. [6], vol. XI. pp. 440-473.

Kingsley, J. S., The Classification of the Arthropoda (Amer. Nat., vol. XXVIII. pp. 118, 220) 1894. Reprinted in Tufts College Studies, No. 1, 1894, with copious bibliography.

the second and third segments, and is frequently strengthened by deposits of carbonate and phosphate of lime. Although the carapace is usually a single piece, yet in some forms (Estheriiform Phyllopods and Ostracods) it may consist of two lateral valves, which enclose the body like a Pelecypod shell; or of four parts, as in certain *Phyllocarida*; or again (*Cirripedia*) of a number of calcareous plates. The abdomen is usually well developed and its segments are free, but occasionally it becomes greatly reduced, as in certain *Entomostraca*.

The total number of body somites varies within wide limits in the *Entomostraca* and Trilobites, but in the *Malacostraca* they are almost constantly twenty-one, ranging slightly higher in the *Phyllocarida*, and falling shorter in the parasitic *Laemodipoda*.

In all living *Crustacea* there are two pairs of antennae, although in some forms (*Apus*, Oniscids) one or the other pair may become greatly reduced. In the Trilobites, on the other hand, but a single pair has been discovered. The appendages are exceedingly variable in form, according as they serve for sensation, comminution of food ("mouth parts"), locomotion, respiration, capture of prey, or copulation. The primitive form was a lamellar appendage like those found in the thoracic region of Phyllopods, but the typical foot is usually stated to consist of a basal portion (*protopodite*) of one or two joints, and a distal portion made up of an inner (*endopodite*) and a lateral branch (*exopodite*). In many cases the exopodite becomes greatly modified or even entirely atrophied in the adult.

Most of the lower *Crustacea* escape from the egg in a larval condition known as the *nauplius stage*. In the nauplius the body is unsegmented, there is but a single median eye, and but three pairs of appendages, corresponding to the two pairs of antennae and mandibles of the adult. The nauplius gradually becomes metamorphosed into the adult Crustacean, the changes being accomplished by several moults of the external chitinous crust. In the higher *Crustacea* this free-swimming nauplius stage is omitted, the animal already having the form of the adult as it escapes from the egg. The Decapods have a larval stage known as the *zoea*, in which seven pairs of appendages and a segmented abdomen are present. These larval stages are of great value in determining relationships, but most modern authorities regard them as adaptive rather than ancestral; or, in other words, it is not believed that existing *Crustacea* are descended from an ancestral form resembling the nauplius.

Two sub-classes are recognised:—*Trilobita* and *Eucrustacea*. The term *Entomostraca* is here used in a collective sense to distinguish the lower orders of *Eucrustacea* from the highest, or *Malacostraca*.

Sub-Class 1. TRILOBITA. Trilobites.[1]

Marine Crustacea, with a variable number of metameres; body covered with a hard dorsal shield or crust, longitudinally trilobate from the defined axis and pleura;

[1] Literature: A. General Works.

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cephalon, thorax, and abdomen distinct. Cephalon covered with a shield composed of a primitively pentamerous middle piece, the cranidium, and two side pieces, or free

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B. Structure and Appendages.

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cheeks, which may be separate or united in front, and carry the compound sessile eyes when present; cephalic appendages pediform, consisting of five pairs of limbs, all biramous, and functioning as ambulatory and oral organs, except the simple antennules, which are purely sensory. Upper lip forming a well-developed hypostoma; under lip present. Somites of the thorax movable upon one another, varying in number from two to twenty-nine. Abdominal segments variable in number, and fused to form a caudal shield. All segments, thoracic and abdominal, carry a pair of jointed biramous limbs. All limbs have their coxal elements forming gnathobases, which become organs of manducation on the head. Respiration integumental and by branchial fringes on the exopodites. Development proceeding from a protonauplius form, the protaspis, by the progressive addition of segments at successive moults.

The Trilobites constitute a group of extinct marine animals, and are related to the stock of the higher modern *Crustacea;* they are therefore to be considered as very primitive Crustaceans. The sub-class had its origin in pre-Cambrian times. Trilobite remains are very abundant in the oldest known fossiliferous strata, the Cambrian, where they exceed in number and diversity all other forms of animal life. They continue to be very plentiful in the Ordovician and Silurian, but decline in the Devonian, and the few last survivors are found in the Carboniferous and Permian. Probably there have been more than two thousand species described, distributed among nearly two hundred genera. These numbers give an idea of the amount of differentiation and specialisation attained by Trilobites during Palaeozoic times.

Carapace.—Trilobites were covered or protected on the dorsal side by a hard crust or shield, which is the only portion commonly preserved. Their remains are therefore readily recognisable by the form and structure of this shield. It is divided longitudinally by two dorsal furrows, or grooves, into three portions or regions, and on this account the name Trilobite was first given. The central part forms the axis of the animal, and contained the principal organs, as the viscera, heart, and chain of ganglia. Transversely the shield is divided into (*a*) a head portion called the cephalon; (*b*) a series of joints or segments, forming the thorax; and (*c*) a tail-piece or pygidium, forming the abdomen.

The test seldom exceeds one millimetre in thickness, and consists of thin laminae of carbonaceous and phosphatic compounds of calcium, some of which were originally chitinous substances. The laminae are frequently traversed by minute pores, which give a punctate appearance to the test, and are sometimes large, as in *Homalonotus* and related forms.

The carapace is somewhat arched or convex, generally elongate-oval in form, and rounded at both ends. The length is almost invariably greater than the width. Very often the same species shows a broad form, as well as a relatively larger, narrower one. The former was considered by Barrande as representing the female, and the latter the male individual. The carapace is often ornamented with spines, teeth, and knobs. These may be of the nature of surface ornaments, or in the case of spines, may be produced by growths from the genal angles, the ends of the segments of the thorax and pygidium, or the spiniform extension of the pygidial termination.

The carapace does not often terminate at the margin as a simple lamellar plate, but is turned under, and forms a reflexed margin, or *doublure*, which is parallel to the outer edge, but is separated from the upper surface by a narrow, partially included space. This produces the hollow spines from the ends of

the segments, the genal angles, and the pygidium. In rare instances, the spines are solid.

The *axis*, or middle part, is defined by two longitudinal dorsal furrows extending the whole length of the thorax, and also over more or less of the cephalon and pygidium.

The *pleura* are the two lateral areas on each side of the axis. Thus, there are pleural cephalic, thoracic, and pygidial regions. The name pleuron or pleura is especially applied to the extensions from the axial portion of each free segment.

The Cephalon.—The cephalon, or cephalic shield (Fig. 1261) includes all that part of the carapace in front of the thorax. It comprises the hypostoma, epistoma, the free cheeks bearing the eyes, the fixed cheeks, and the glabella; it is generally semicircular in form, and is joined along its posterior margin to the thorax. The postero-lateral margins, or genal angles, are frequently drawn out into spines. Usually there is an occipital furrow extending across the cephalon parallel to the posterior margin, and defining the occipital ring or segment.

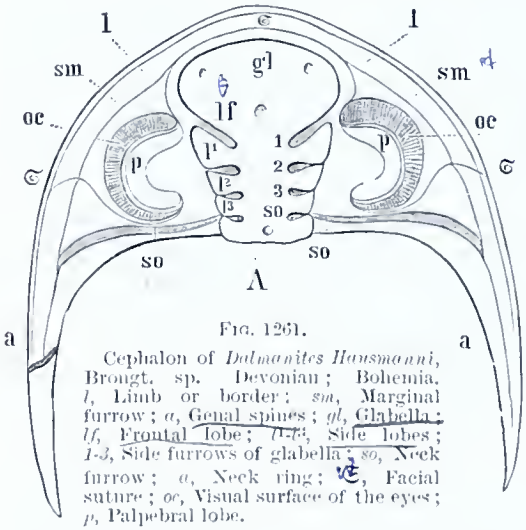


Fig. 1261.

Cephalon of *Dalmanites Hausmanni*, Brongt. sp. Devonian; Bohemia. *l*, Limb or border; *sm*, Marginal furrow; *a*, Genal spines; *gl*, Glabella; *lf*, Frontal lobe; *1-3*, Side lobes; *1-3*, Side furrows of glabella; *so*, Neck furrow; *a*, Neck ring; *c*, Facial suture; *oc*, Visual surface of the eyes; *p*, Palpebral lobe.

The *glabella* is the axial portion of the cephalon, and is defined by the primary dorsal furrows (Fig. 1261). It shows typically three oblique or transverse furrows in addition to the occipital ring, marking the limits of the original five consolidated segments, and corresponding to the paired appendages of the ventral side. Sometimes the positions of the muscular fulcra are also indicated on the dorsal surface, by short furrows, or by shallow pits. The glabella may constitute nearly the whole of the cephalon, as in *Deiphon* or *Aeglina*, or it may be narrow, as in *Harpes*, and *Euryeare*. In some cases it does not extend over half the length of the cephalon, as in *Harpes* and *Arethusina*, but it may extend to the frontal border, as in *Placoparia* or *Calymmene*, or even beyond, as in *Phacops*, *Ampyx*, and *Conolichas*. The entire portion of the glabella which lies in front of the anterior lateral furrows, and which is often somewhat enlarged laterally, is called the frontal lobe. At times the limitation between the glabella and fixed cheeks is scarcely defined, as in *Illaenus* and *Dipleura*. Most frequently, however, three pairs of grooves can be distinguished in front of the neck furrow, marking the pentamerous division of the glabella and the five pairs of appendages attached to the cephalon. Sometimes the lateral furrows are continuous across the glabella, or again, they may be directed obliquely (*Triarthrus*), or even form longitudinal grooves (*Conolichas*).

The *hypostoma*, or labrum, is homologous to the upper lip of other Crustaceans, and consists of a separate plate attached by an articulating surface or line to the reflexed border of the cephalic shield (Figs. 1262, 1265, *B*).

In front of the hypostoma is a rostral area sometimes partly occupied by a separate plate.

The *fixed cheeks* are lateral extensions from the glabella, to which they are firmly joined, forming the central portion of the cephalon. They may occupy more than two-thirds of the cephalon, as in *Conocoryphe*, or become greatly reduced, as in *Asaphus*, *Lichas*, and *Proëtus*. The *cranidium* consists of the glabella and the fixed cheeks.

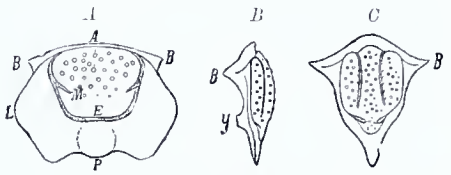


Fig. 1262.

Hypostomas. *A*, *Lichas* (*Arges*) *palmata*. *B*, *C*, *Encrinurus intercostatus*, side and front views (after Novák). *BB*, Anterior edge; *M*, Middle furrow; *E*, Posterior furrow of the middle portion; *P*, Posterior edge; *L*, Lateral edge; *y*, Posterior wing.

The *free cheeks* carry the compound eyes, and are separated from the cranidium by a suture. They may form (*a*) a continuous ventral plate, as in *Harpes*, *Agnostus*, *Trinucleus*, etc.; they may include (*b*) a greater or lesser portion of the dorsal surface, being either entirely separated by the cranidium, or (*c*) meeting and (*d*) sometimes coalescing in front. They are widely separated in *Ptychoparia*, in juxtaposition in *Asaphus*, and continuous in *Dalmanites*.

The *genal angles* are the posterior lateral angles of the cephalon. They may be rounded, as in *Illaenus*, angular, as in *Bronteus*, or spiniform, as in *Trinucleus* and *Dalmanites*. They belong either to the fixed cheeks, as in *Dalmanites*, or to the free cheeks, as in *Illaenus*, *Bronteus*, and *Proëtus*.

The character of the cheeks is especially influenced by the facial sutures separating the free cheeks from the rest of the cephalon. They appear as sharply defined lines beginning either at the posterior margin, or near the genal angles, or on the lateral margins, and extend to the eyes, thence around the inner margin of the visual areas, then turn anteriorly, and either unite in passing around the front of the glabella or remain separate, in which case the sutures terminate in the anterior margin. The position of the facial sutures thus determines the relative size of the fixed and free cheeks. After the death of the animal, or after moulting, the cephalic shield frequently fell into pieces, dividing along these sutures.

In most Trilobites, the existence of eyes has been demonstrated, though they appear absent altogether in some genera (*Conocoryphe*, *Agnostus*), and are so imperfectly shown in others that for a long time they remained unrecognised (*Agraulus*, *Sao*, *Ellipsocephalus*, etc.). The eyes are compound, and are elevated above the free cheeks. The adjoining area of the fixed cheeks is also drawn upwards, thus forming the palpebral lobe. The visual areas of the eyes are borne by the free cheeks. The shape of this area is extremely variable, but together with the palpebral lobe it generally forms a truncated, conical, or semilunar elevation, of which the laterally directed, convex side is occupied by the visual area (*Phacops*, *Asaphus*). It may likewise have a circular or oval form, and very little convexity above the general surface. The eyes may be quite small, as in *Encrinurus* and *Trimerocephalus*; large and prominent, as in *Phacops*, *Dalmanites*, and *Proëtus*; or very large, as in *Aeglina*, in some species of which nearly the entire area of the free cheeks is faceted, and the visual surface extends around the entire outer borders of the cephalon. In many of the primitive genera the eyes are situated at the distal ends of raised lines, or *eye lines*, extending outward from near the forward end of the glabella.

As regards their structure, the compound eyes of Trilobites are recognised

as of two kinds. In the first, the *holochroal*, the visual area is covered with a continuous horny integument, or cornea, which is either smooth and externally gives no idea of its compound nature, or granular, on account of the facets beneath. The lenses of the ommatidia are often visible by translucence. The second type of structure, the *schizochroal*, is confined to the single family *Phacopidae*. In this, the visual area is made up of small, round, or polygonal openings for the separate facets of the cornea, between which is an interstitial test or sclera. The size of the facets varies from more than 0·5 mm. in some of the *Phacopidae*, to from 6-14 in the width of 1 mm. in other Trilobites. The number and arrangement of the facets also vary greatly according to the genus. *Trimerocephalus Volborthi* shows only 14 facets, while species of *Phacops* may possess from 200-300, and *Dalmanites Hausmanni* has 600. Among the holochroal eyes, the number of facets is much greater; in *Bronteus palifer* it is estimated at 4000, in *Asaphus nobilis*, and in *Remopleurides radians* as high as 15,000. Usually the facets are arranged in regular, alternating, vertical rows, or quincuncially.

Certain genera show visual organs of an entirely different type, which can be best regarded as simple eyes, and correlated with the ocelli of many Crustaceans. Thus, the genus *Harpes*, and some species of *Trinucleus* present from one to three simple elevations or granules on the fixed cheeks, at the ends of eye-lines, while the ordinary compound eyes on the free cheeks are absent.

The Thorax.—In contrast to the undivided cranidium, the thorax consists of a series of short, transverse, articulating segments, which vary in number with the genus. Every thoracic segment is divided by the dorsal furrows into a middle portion (*axis*, *tergum*) and two lateral divisions (*pleura*, *epimera*). The axial portions are firmly anchylosed with the pleura, and are generally strongly convex, with the posterior margin incurved. Anteriorly they bear an extension below the general surface, and separated by a furrow. This forms a surface of articulation along which the segments are movable, and is covered by the edge of the segment immediately in front, so that it is chiefly visible in coiled or disarticulated specimens. Barrande distinguished two types of pleura: (*a*) furrowed pleura (*plèvre à sillon*), which have a diagonal furrow on the upper surface, running posteriorly from the anterior edge near the axis, and towards the free extremity; and (*b*) ridged pleura (*plèvre à bourrelet*), having a longitudinal ridge or narrow fold. These characters vary considerably, and are sometimes obscure. In a small number of genera (*Illaenus*, *Nileus*) the pleura are perfectly smooth.

All pleura show a distal or lateral, and a proximal or inner portion. The latter extends from the axis to the fulcrum or bend, *i.e.* to a place where the pleura bend more or less abruptly downward, and also generally toward the rear. The distal portion, beginning at the fulcrum, may continue of equal thickness and be rounded or obtuse at the extremity, or it may decrease in size and terminate in a spine.

The number of thoracic segments varies exceedingly among different genera. The smallest number (2) occurs in *Agnostus*. The largest number so far observed (29) is found in some species of *Harpes*. A variation is to be noted even among the species of a single genus, hence this character is not of general application for purposes of classification. For example, there are species of *Ampyx* and *Aeglina* with five to six thoracic segments, *Phillipsia* with nine to fifteen, *Cheirurus* with ten to twelve, *Cyphaspis* with ten to seventeen,

Ellipsocephalus with ten to fourteen, and *Paradoxides* with sixteen to twenty. In general, there seems to be a sort of mutual relationship between the number of thoracic segments and the size of the pygidium. When the latter is large, the thoracic segments are usually few; but if small, the number of segments is large.

The Pygidium.—The abdomen of Trilobites is commonly known as the *pygidium* (Fig. 1263), though sometimes styled the caudal shield or plate. It consists of a single piece, with an arched upper surface, upon which may be distinguished regularly a median axis and two lateral parts, or pleural limbs, marked more or less distinctly by transverse furrows. Sometimes it bears considerable resemblance to the cephalic shield (*Agnostus*, *Microdiscus*). The

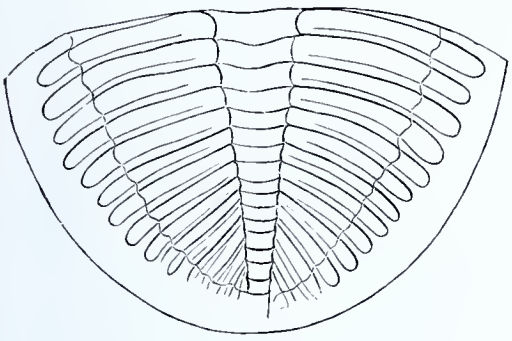


Fig. 1263.

Pygidium of *Oggyia Buchi*, Brongt. Ordovician, Wales.

Fig. 1264.

Pygidium of *Bronteus umbellifer*, Beyr. Devonian; Bohemia.

pygidium evidently originated from the anchylosis of a number of similar segments. The potential segmentation is often so strongly marked that it is very difficult to recognise the dividing line between the thorax and pygidium, except in disarticulated specimens. Sometimes the evidences of segmentation disappear entirely or are but faintly indicated on the lower side. When segmentation along the axial and lateral lobes is weak, the pygidium varies considerably in appearance from the thorax.

The *axis* may extend as far as the posterior end of the pygidium, or to any part of the length, but is sometimes reduced to a short rudiment (*Bronteus*, Fig. 1264), or it may be even entirely obscured (*Nileus*). The number of axial segments normally corresponds to the number of pygidial, and varies between two and twenty-eight. On the lateral lobes, all or at least a part of the pleura may also be seen, being continued from the axis as ribs separated by furrows. In these cases, the furrowed and the ribbed pleura can usually be distinguished, but not infrequently they have entirely disappeared as surface features. Many of the Cambrian Trilobites are conspicuous for their small pygidium and elongated thorax.

The outline of the pygidium is most frequently semicircular, parabolic, or elliptical; more rarely it is triangular or trapezoidal. The margin is entire, less commonly dentate or spiny. The border, as in the case of the cephalon and the pleura of the segments, has a reflexed margin, or doublure, which in some genera attains considerable width.

The Ventral Side.—The ventral side of Trilobites is commonly inaccessible for purposes of observation, since, as a rule, it is so firmly attached to the

rock that the organs, even though present, cannot be exposed by the ordinary methods. Furthermore, the appendages and ventral structures are so thin and delicate that the most favourable conditions are necessary for their preservation. For this reason, great uncertainty has prevailed regarding the presence and character of the legs and various appendages. After a careful preparation of their inferior side, by far the larger number of Trilobites show only the vacant hollow space beneath the dorsal shell, and the hypostoma attached to the reflexed margin of the cephalic shield, as represented in Fig. 1266. This common condition of the fossils led Burmeister, in 1843, to the assumption that all organs on the lower side, as in Phyllopods, were originally soft and fleshy. Previous to this, however, Linnaeus, in 1759, described what appeared to be antennae, and Eichwald, in 1825, announced both antennae and legs. Altogether the early literature down to 1870 contains quite a number of claimants for this discovery. Most of the evidence is manifestly erroneous, and the two or three cases which bear some semblance of validity are too obscure to be of any scientific value.

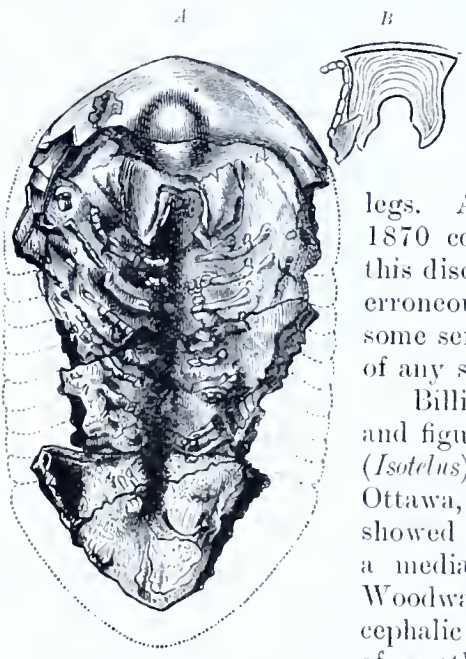


Fig. 1265.

Asaphus (*Isotelus*) *gigas*, De Kay. Ordovician; Ottawa, Canada. *A*, Ventral side, showing remains of jointed feet (after Billings). *B*, Hypostoma with antenna or pediform cephalic appendage (after Woodward).

Billings, in 1870, published the description and figure of an unusually well-preserved *Asaphus* (*Isotelus*) *gigas* from the Trenton limestone of Ottawa, Canada. The ventral side of the specimen showed eight pairs of jointed feet on each side of a median furrow (Fig. 1265, *A*). Soon after, Woodward described an antenna or pediform cephalic appendage, lying beside the hypostoma of another individual of the same species (Fig. 1265, *B*). Through the investigations of Walcott (1875-94) on *Ceraurus* and *Calymmene*, by means of transverse and longitudinal sections of enrolled specimens, a number of problems have been settled as to the characters of the ventral side. According to these investigations, Trilobites possessed a thin, external, ventral membrane attached to the reflexed margin of the cephalon, the thoracic segments, and pygidium. It was supported by transverse processes which became calcareous with age, and to these the feet were attached.

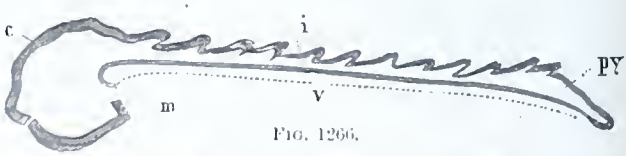


Fig. 1266.

Median vertical section of *Ceraurus pleurexanthemus*, Green. *c*, Cephalon with hypostoma below; *m*, Mouth; *v*, Ventral membrane; *i*, Intestinal canal; *py*, Pygidium (after Walcott).

The intestinal canal, discovered by Beyrich and Volborth, is located beneath the axial lobe, within the visceral cavity. It begins at the mouth, which Walcott found at the posterior margin of the hypostoma, first bends forward toward the dorsal region, and then extends backward from the glabella to the posterior end of the pygidium, and parallel to the dorsal test, terminating in the anal opening (Fig. 1266).

Most of the recent advances in the knowledge of Trilobite structure have come from the study of numerous very perfectly preserved specimens of *Triarthrus Becki*, Green, from the Utica Slate (Ordovician), near Rome, New York. Undoubted antennae in this form were discovered by Valiant, and first announced by Matthew in 1893. Subsequently a series of papers was published by Beecher on the detailed structure of this Trilobite, which is now

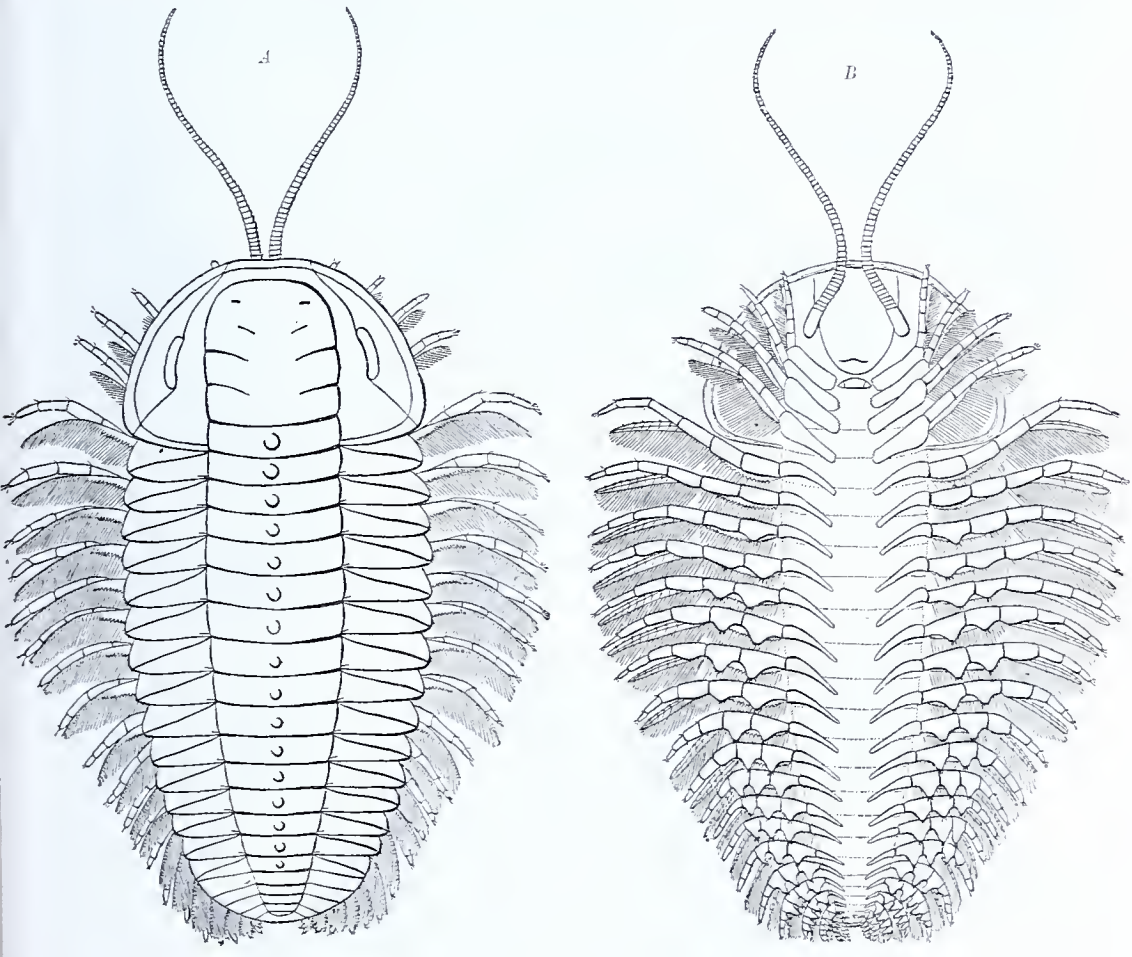


FIG. 1267.

Triarthrus Becki, Green. Utica Slate (Ordovician); Rome, New York. *A*, Dorsal, and *B*, Ventral aspect, 2/1 (after Beecher).

the best known of any species, and necessarily forms the basis of much of the following summary of ventral organs.

In the median line anteriorly, there is first the hypostoma or upper lip, at the end of which, and opening obliquely backward, is the mouth (Walcott, in *Calymmene*). In *Triarthrus* the lower lip, or metastoma, is a convex arcuate plate, just posterior to the extremity of the hypostoma. At the angles on either side are two small elevations, or lappets.

Paired Appendages.—All segments of the cranidium, thorax, and pygidium, except the anal segment, carry paired appendages, which are all biramous save the anterior pair. The anterior antennae, or antennules, are attached at the sides of the hypostoma, and consist of a simple, many-jointed flagellum (Fig. 1267).

The normal Trilobite leg has two branches arising from a basal joint, or *coxopodite*, which is prolonged into a *gnathobase*. The inner branch, or *endopodite*, has normally six joints. The outer branch, or *exopodite*, has a long proximal joint, with a distal multiarticulate portion. Long setae extend posteriorly, and on the distal portion they are so crowded as to make a conspicuous fringe, imparting a characteristic appearance to the leg.

Besides the antennules, the cephalon bears four pairs of pediform biramous appendages, with large gnathobases functioning as manducatory organs. Of

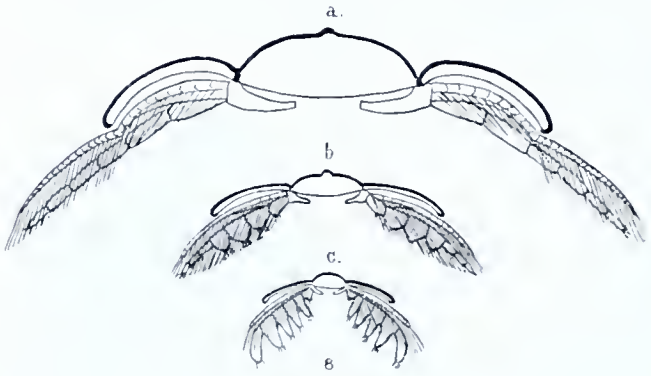


Fig. 1268.

Triarthrus Becki, Green. *a*, Restored thoracic limbs in transverse section of the animal; *b*, Section across anterior portion of pygidium; *c*, Section across posterior portion of pygidium (after Beecher).

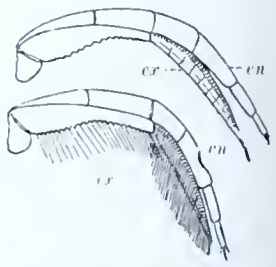


Fig. 1269.

Triarthrus Becki, Green. Dorsal view of second thoracic leg, with and without setae and without gnathobase. *en*, Endopodite; *ex*, Exopodite (after Beecher).

these the first may be correlated with the posterior antennae of higher *Crustacea*. In structure and function they are true mouth appendages, like the second

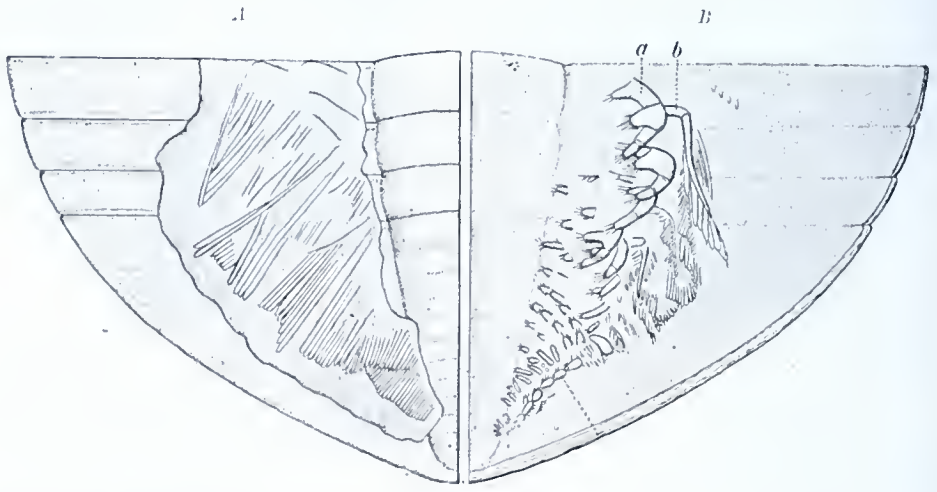


Fig. 1270.

Trinucleus concentricus, Eaton. Utica Slate (Ordovician); Rome, New York. *A*, Left half of pygidium and three thoracic segments, with test removed, and showing fringes of the exopodites. *B*, Ventral aspect of same. *a*, Endopodite; *b*, Exopodite. [10/1] (after Beecher).

pair of nauplius limbs. The second pair, corresponding to the mandibles of higher forms, and the third and fourth, corresponding to maxillae, have the same structure as the first, with large gnathobases and fringed exopodites. The thoracic and abdominal limbs are of the same biramous type. The endopodites are jointed, crawling legs; posteriorly, especially on the pygidium,

the joints become flattened and leaf-like, carrying tufts of setae, and being adapted for swimming.

The exopodites are fringed along their posterior edges with narrow, oblique lamellar elements becoming filiform at the ends, thus converting the limb into a swimming organ, and also serving respiratory functions (Figs. 1267, 1270).

Habits.—In the absence of any closely allied recent forms, it is difficult to reach definite conclusions respecting the manner of life of Trilobites, except such as are based upon their organisation and mode of occurrence. They were undoubted marine animals, since their remains are found only in salt-water deposits, associated with Brachiopods, Cephalopods, Crinoids, and other typical oceanic forms. Some species are plentiful in calcareous or argillo-calcareous deposits, with thick-shelled Brachiopods, Gastropods, and reef-building Corals, which evidently did not live at any considerable depth. Other forms appear to have been bottom crawlers, frequenting either muddy or sandy bottoms; and again, others like *Trinucleus*, lived partly buried in the soft mud. On the other hand, many species indicate, from the absence of visual organs, a comparatively deep-water habitat. The structure of the appendages of many was probably such as to permit of both swimming and crawling, as in a number of families of modern *Crustacea*, and they were therefore restricted neither to the shore nor to the bottom. This doubtless explains the occurrence of the same species in very different sediments.

Power of Enrolment.—The bodies of most Trilobites were capable of being rolled up completely like many of the Isopods (Fig. 1271). In the enrolled condition the margin of the pygidium is closely applied to the doublure of the cephalon, thus entirely concealing the ventral side of the body. The thoracic segments overlap, and admit of more or less motion upon one another. The pleura also imbricate, and their fulcra are provided with facets upon which the fulcra of adjacent segments impinge. The ends of the pleura thus protect the ventral surface along the sides, when the animal is enrolled. Some forms appear to have possessed the power only to a limited degree. In these, the creature is usually found extended, and the facets on the fulcra are either rudimentary or absent.

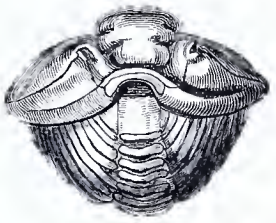


Fig. 1271.

Calymmene senaria, Conrad. Ordovician; Cincinnati, Ohio. Enrolled specimen.

Ontogeny.—Minute spherical or ovoid fossils associated with Trilobites have been described as possible Trilobite eggs, but nothing is known, of course, of the embryonic stages of the animals themselves. The smallest and most primitive organisms which have been detected, and traced by means of a series of specimens through successive changes into adult Trilobites, are little discoid or ovate bodies not more than 1 mm. in length. This first larval form has been named the *protaspis* (Beecher), and has been found to be the normal larval type characteristic of all Trilobites. It is believed to approximate the protonauplius form, or the theoretical, primitive, ancestral, larval form of the *Crustacea*.

The simple characters possessed by the protaspis are the following, as drawn from the study of this stage in all the principal groups of Trilobites:—*Dorsal shield minute, not more than* 0·4 *to* 1 mm. *in length; circular or ovate in form; axis distinct, more or less strongly annulated, limited by longitudinal grooves;*

head portion predominating; axis of cranidium with five annulations; abdominal portion usually less than one-third the length of the shield; axis with from one to several annulations; pleural portion smooth or grooved; eyes, when present, anterior marginal, or submarginal; free cheeks, when visible, narrow and marginal.

The changes taking place during the growth of an individual are chiefly the following:—Elongation of the body through the gradual addition of the free thoracic segments; translation of the eyes, when present; modifications in the glabella; growth of the free cheeks; and final assumption of the mature specific characters of pygidium and ornamentation.

In a classification of the stages of growth, the protaspis has the rank of a phylembryo, and corresponds in value to the protoconch of Cephalopods, the prodissoconch of Pelecypods, and the protegulum of Brachiopods. In its geological history and the metamorphoses it undergoes to produce the perfect Trilobite, accurate information can be gained as to what the primitive characters are, and the relative values of other features acquired during the long existence of the class.

Of the stages of growth after the protaspis, the nepionic may be considered as including the animal when the cephalon and pygidium are distinct, and the

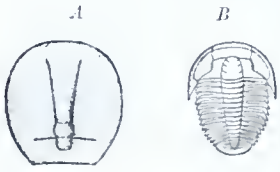


Fig. 1272.

Ptychoparia Kingi, Meek. Cambrian. *A*, Protaspis enlarged. *B*, Adult reduced.

Fig. 1273.

Sao hirsuta, Barr. Cambrian. *A*, Protaspis enlarged. *B*, Adult reduced.

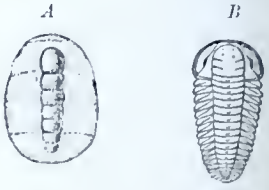


Fig. 1274.

Triarthrus Becki, Green. Ordovician. *A*, Protaspis enlarged. *B*, Adult reduced.

thorax incomplete. There would thus be as many nepionic stages as there are thoracic segments. The neanic stages would be represented by the animal with all parts complete, but with the average growth incomplete.

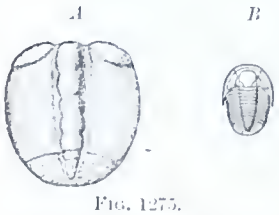


Fig. 1275.

Proetus parciuscalus, Hall. Ordovician. *A*, Protaspis much enlarged. *B*, Adult slightly enlarged.

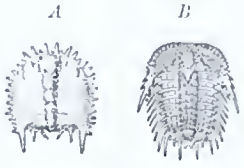


Fig. 1276.

Acidaspis tuberculata, Conrad. Devonian. *A*, Protaspis enlarged. *B*, Adult reduced.

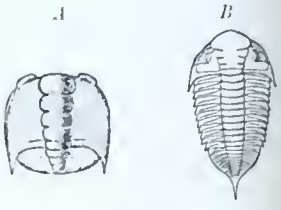


Fig. 1277.

Dalmanites socialis, Barr. Ordovician. *A*, Protaspis enlarged. *B*, Adult reduced. (Figs. 1272-77 after Beecher.)

Final progressive growth and development of the individual would fall under the ephebic stage. Lastly, general evidences of senility would be interpreted as belonging to the gerontic stage.

Morphogeny.—During the protaspis stage, several moults take place before the complete separation of the pygidium or the introduction of thoracic segments. These bring about various changes, namely, the stronger annulation of the axis, the appearance of the free cheeks on the dorsal side, and development of the pygidium by the introduction of new appendages and segments,

as indicated by the additional grooves on the axis and limb. In the earliest, or Cambrian genera, the protaspis stage is by far the simplest expression of this period to be found. In the higher and later genera, the process of acceleration or earlier inheritance has pushed forward certain characters until they appear in the protaspis, thus making it more and more complex.

Taking the early protaspis stages in *Solenopleura*, *Liostracus*, or *Ptychoparia*, it is found that they agree exactly with the foregoing diagnosis in its most elementary sense. Since they are the characters shared in common by all larvae at this stage, they are taken as primitive, and accorded that value in dealing with adult forms possessing homologous features. Therefore, any Trilobite with a large elongate cephalon, eyes rudimentary or absent, free cheeks ventral or marginal, and glabella long, cylindrical, and with five annulations, would naturally be placed near the beginning of any genetic series, or as belonging to a very primitive stock.

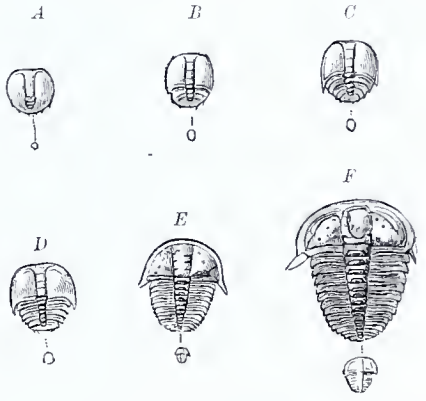


FIG. 1278.

Sao hirsuta, Barr. Cambrian; Skrey, Bohemia. *A*, Protaspis. *B-F*, Nepionic stages of development (after Barrande).

Next must be considered the progressive addition of characters during the geological history of the protaspis, and the ontogeny of the individual during its growth from the larval to its mature condition. It has been shown by Beecher that there is an exact correlation to be made between the geological and zoological succession of first larval stages and adult forms, and therefore both may be reviewed together.

The first important structures not especially noticeable in all stages of the protaspis are the free cheeks, which usually manifest themselves in the meta- or para-protaspis stages, though sometimes even later. Since they bear the visual areas of the eyes, when such are present, their appearance on the dorsal shield is practically simultaneous with these organs, and before the eyes have travelled over the margin, the free cheeks must be wholly ventral in position. When first discernible, they are very narrow, and in *Ptychoparia* and *Sao*, include the genal angles. In *Dalmanites* and *Cheirurus*, however, the genal angles are borne on the fixed cheeks.

Since the free cheeks are ventral in the earliest larval stages of all but the highest Trilobites, and as this is an adult feature among a number of genera, which on other grounds are very primitive, this is taken as generally indicative of a very low rank. The genera *Harpes*, *Agnostus*, *Trinucleus*, and their allies agree in this respect, and constitute the *Hypoparia*.

The remaining genera of Trilobites present two distinct types of head structure, dependent upon the extent and character of the free cheeks. In both, the free cheeks make up an essential part of the dorsal crust of the cephalon, being continued on the ventral side only as a doublure or infolding of the edge, similar to that of the free edge of the cranidium, the ends of the thoracic pleura, and the margin of the pygidium. They may be separated only by the cranidium, as in *Ptychoparia;* by the cranidium and separate epistomal or rostral plate, as in *Illaenus* and *Homalonotus;* or they may be united and continuous in front, as in *Aeglina* and *Dalmanites*. One type of

structure is distinguished by having the free cheeks include the genal angles, thus cutting off more or less of the pleura of the occipital segment. The genera belonging to this group constitute the second order—the *Opisthoparia*.

The third and last type of structure includes forms in which the pleura of the occipital segment extend the full width of the base of the cephalon, embracing the genal angles. The free cheeks are therefore separated from the

FIG. 1279.

Ontogeny of *Sao hirsuta*, Barr. (*Opisthoparia*) *A*, Protaspis. *B*, Cephalon of nepionic individual. *C*, Cephalon of later nepionic individual having eight free segments. *D*, Cephalon of adult (from Beecher, after Barrande).

cranidium by sutures cutting the lateral margins of the cephalon in front of the genal angles. Genera having this structure are here placed in the order *Proparia*.

The characters still to be noticed have chiefly family and generic values, and are of great assistance both in determining the place of a family in an order and the rank and genetic position of a genus in a family.

There is very satisfactory evidence that the eyes have migrated from the ventral side, first forward toward the margin, and then backward over the

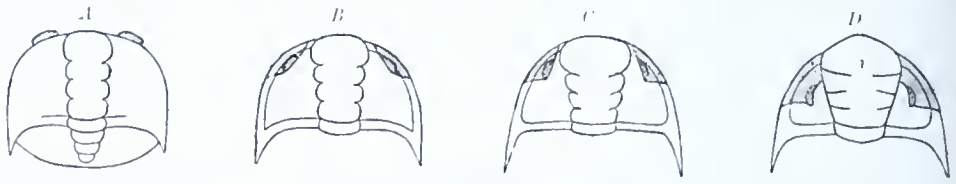


FIG. 1280.

Ontogeny of *Dalmanites socialis*, Barr. (*Proparia*) *A*, Protaspis. *B*, Cephalon of individual of three free segments. *C*, Cephalon of one of seven free segments. *D*, Cephalon of adult (from Beecher, after Barrande).

cephalon to their adult position. The most primitive larvae should therefore present no evidence of eyes on the dorsal shield. Just such conditions are fulfilled in the youngest larvae of *Ptychoparia*, *Solenopleura*, and *Liostracus*. The eye-line is present in the later larval and adolescent stages of these genera, and persists to the adult condition. In *Sao* it has been pushed forward to the earliest protaspis, and is also found in the two known larval stages of *Triarthrus*. *Sao* retains the eye-line throughout life, but in *Triarthrus* the adult has no trace of it. A study of the genera of Trilobites shows that this is a very archaic feature, chiefly characteristic of Cambrian genera, and only appearing in the primitive genera of higher and later groups. It first develops in the later larval stages of certain genera (*Ptychoparia*, etc.); next in the early larval stages (*Sao*); then disappears from the adult stages (*Triarthrus*); and finally is pushed out of the ontogeny (*Dalmanites*).

In *Ptychoparia*, *Solenopleura*, *Liostracus*, *Sao*, and *Triarthrus*, the eyes are first visible on the margin of the dorsal shield after the protaspis stages have been passed through, and later than the appearance of the eye-lines; but in *Proetus*, *Acidaspis*, *Arges*, and *Dalmanites*, through acceleration, they are present in all the protaspis stages, and persist to the mature or ephebic condition,

moving in from the margin to near the sides of the glabella. Progression in these characters may be expressed, and in so far taken for general application among adult forms to indicate rank, as follows :—(1) Absence of eyes ; (2) eye-lines ; (3) eye-lines and marginal eyes ; (4) marginal eyes ; (5) submarginal eyes ; (6) eyes near the pleura of the neck segment.

The changes in the glabella are equally important and interesting. Throughout the larval stages the axis of the cranidium shows distinctly by the annulations that it is composed of five fused segments, indicating the presence of as many paired appendages on the ventral side. In its simplest and most primitive state it expands in front, joining and forming the anterior margin of the head (larval *Ptychoparia* and *Sao*). During later growth it becomes rounded in front, and terminates within the margin. In higher genera, through acceleration, it is rounded and well-defined in front, even in the earliest larval stages, and often ends within the margin (larval *Triarthrus* and *Acidaspis*). From these few simple types of pentamerous glabellae, all the diverse forms among species of various genera have been derived, through changes affecting any or all of the lobes. The modifications usually consist in the progressive obsolescence of the anterior annulations, finally producing a smooth glabella, as in *Illaenus* and *Niobe*. The neck segment is the most persistent of all, and is rarely obscured. The third, or mandibular segment is frequently marked by two entirely separate lateral lobes, as in *Acidaspis*, *Conolichas*, *Chasmops*, etc. Likewise, the fourth annulation carrying the first pair of maxillae is often similarly modified in the same genera, also in all the *Proëtidae*, and in *Cheirurus*, *Crotalocephalus*, *Sphaerexochus*, *Ampyx*, *Harpes*, etc. Here, again, among adult forms, the stages of progressive differentiation may be taken as indicating the relative rank of the genera.

The comparative areal growth of the free cheeks is expressed by the gradual moving of the facial suture toward the axis. As the free cheeks become larger the fixed cheeks become smaller. In the most primitive protaspis stages, and in *Agnostus*, *Harpes*, and *Trinucleus*, the dorsal surface of the cephalon is wholly occupied by the axis and fixed cheeks, while in the higher genera the area of the fixed cheeks becomes reduced until, as in *Stygina* and *Phillipsia*, they form a mere border to the glabella. Therefore the ratio between the fixed and free cheeks furnishes another means of assisting in the determination of rank.

The pleura from the segments of the glabella are occasionally visible, as in the young of *Elliptocephala*, but usually the pleura of the neck segments are the first and only ones to be distinguished on the cephalon, the others being so completely coalesced as to lose all traces of their individuality. The pleura of the pygidium appear soon after the earliest protaspis stage, and in some genera (*Sao*, *Dalmanites*) are even more strongly marked than in the adult state, and much resemble separate segments. The growth of the pygidium is very considerable through the protaspis stage. At first it is less than one-third the length of the dorsal shield, but by successive addition of segments it soon becomes nearly one-half as long. In some genera it is completed before the appearance of the free thoracic segments, all of which are added during the nepionic stages. An interpretation of these facts, to apply in valuing adult characters, would indicate that a very few segments, both in thorax and pygidium, may be evidence of arrested development or suppression. On the other hand, the apparently unlimited multiplication of thoracic and especially

of abdominal segments in some genera is also to be considered as a primitive character expressive of an annelidan style of growth. Genera, like *Asaphus*, *Phacops*, etc., having a constant number of thoracic segments accompanied by other characters of a high order, undoubtedly represent the normal Trilobite type.

These analyses and correlations clearly show that there are characters appearing in the adults of higher and later genera, which successively make their appearance in the protaspis stage, sometimes to the exclusion or modification of structures present in the more primitive larvae. Thus the larvae of *Dalmanites* or *Proëtus*, with their prominent eyes and glabella distinctly terminated and rounded in front, have characters which do not appear in the larval stages of ancient genera, but which may come in their adult stages. Evidently such modifications have been acquired by the action of the law of earlier inheritance or tachygenesis.

Position in the Zoological System.—Since Trilobites have been made the subject of special study, they have been commonly classed with the *Crustacea*, and placed near the Phyllopods by most observers. Quite a number of naturalists, however, still divorce the Trilobites and Limuloids from the *Crustacea*, and ally them with the Arachnids. Leaving aside the question of the homologies of *Limulus*, it is a fact that Trilobites show the clearest evidence of primitive Crustacean affinities, in their protonauplius larval form, their hypostoma and metastoma, the five pairs of cephalic appendages, the slender jointed antennules, the biramous character of all the other limbs, and their original phyllopodiform structure. They differ from *Limulus*, not only in most of these respects, but also in not having an operculum. From *Limulus* and all other Arthropods they are distinguished by having compound eyes on free cheek-pieces, which apparently represent the pleura of a head segment that is otherwise lost, except possibly in some forms of stalked eyes and in the cephalic neuromeres of later forms. The most recent discussions as to the affinities of Trilobites are to be found in the papers by Bernard, Kingsley, Woodward, and Beecher, where, from the facts presented, the relationships of these animals with the *Crustacea* follow as a necessary corollary.

As to the rank of the Trilobites in a classificatory scheme, there is also much diversity of opinion. They have been long regarded as an order of Crustaceans, but any attempt to include them in this way under higher groups, such as the *Entomostraca*, *Malacostraca*, or *Merostomata*, results in such broad generalities and looseness of definition as to render these divisions of little value. The present state of knowledge of Trilobite structure and development is in favour of assigning them nothing short of the rank of a sub-class.

In nearly every particular, the Trilobite is very primitive, and closely agrees with a theoretical Crustacean ancestor. Its affinities are with the known sub-classes of the group, especially their lower orders, but its position is not intermediate. The more primitive characters may be summarised as follows:—(1) They are all free marine animals; (2) they have a definite configuration; (3) the larva is a protonauplius-like form; (4) the body and abdomen are richly segmented, and the number of segments is variable; (5) the head is typically pentamerous; (6) the thorax and abdomen are always distinct, the number of segments in each being variable; (7) all segments except the anal bear paired appendages; (8) all appendages except antennules

are biramous; and (10) the coxal elements of all limbs form gnathobases, which become organs of manducation on the head.

Classification.—Barrande gives a complete résumé of the classifications applied to Trilobites down to 1850, and shows in a very satisfactory manner the weak points of each, furnishing strong reasons as to why they are unnatural and therefore untenable. The underlying principles of these early attempts at a classification are here briefly summarised. (1) The first classification of Trilobites was advanced by Brongniart in 1822, in which all the forms previously known as *Entomolithus paradoxus* were shown to belong to five distinct genera. (2) Dalman, 1826, made two groups, based upon the presence or absence of eyes. (3) Quenstedt, 1837, recognised the number of thoracic segments and the structure of the eyes as of the greatest importance. (4) Milne-Edwards, 1840, considered the power of enrolment as of prime value. (5) Goldfuss, 1843, established three groups depending on the presence or absence of eyes and their structurae. (6) Burmeister, 1843, accepted the two divisions of Milne-Edwards, and laid stress on the nature of the pleura and the size of the pygidium. (7) Emmrich's first scheme, 1839, was founded on the shape of the pleura, the presence or absence of eyes and their structure. (8) The later classification of the same author, published in 1844, depended on whether the abdomen was composed of fused or free segments, and the minor divisions were based chiefly on the structure of the eyes and the facial suture. (9) Corda, 1847, placed all Trilobites in two groups, one having an entire pygidial margin, and the other with the pygidium lobed or denticulate. (10) M'Coy, 1849, took the presence or absence of a facet on the pleura for a divisional character. As this is an indication of the relative power of enrolment, it does not differ materially from the schemes of Milne-Edwards and Burmeister. Zittel, in a review brought down to 1885, includes in addition the schemes of (11) Barrande, 1850, and (12) Salter, 1864, and remarks that the basis of Barrande's general grouping, namely, the structure of the pleura, has neither a high physiological nor a morphological significance. Both Barrande and Salter recognise nearly the same families, with slight differences, and the latter adopts a division into two lines, based on the number of body rings and size of the pygidium. These include and are themselves included in four groups, founded on the presence and form of the facial suture and the structure of the eyes. (13) Chapman, in 1889, proposed four sub-orders or primary groups based purely upon arbitrary features of general structure and configuration, especially the form of the glabella, whether wide, conical, or enlarged. (14) Haeckel, in 1896, divided the Trilobites into two orders based upon the presence or absence of a functional pygidium.

In the classification here adopted, the families as defined by Salter and Barrande are in the main adhered to, and the number corresponds very closely with that in Zittel's *Handbuch der Palaeontologie*, and also with that in the *Grundzüge* of the same author. The ordinal divisions, and the definitions and arrangements of families, are taken from the classification prepared by Beecher in 1897, based upon the study of ontogeny and morphogenesis, as already shown.

Order 1. HYPOPARIA. Beecher.

Free cheeks forming a continuous marginal ventral plate of the cephalon, and in some forms also extending over the dorsal side at the genal angles. Suture ventral

marginal, or submarginal. Compound paired eyes absent; simple eyes may occur on each free cheek, singly or in pairs.

Even in the higher genera of this order, the suture is frequently unnoticed, but can be seen in all well-preserved specimens. In *Trinucleus* and *Harpes* it follows the edge of the cephalon, and separates the dorsal from the ventral plate of the pitted limb. Since eye-spots occur on the fixed cheeks in the young of *Trinucleus* and adult *Harpes*, it is probable that this character is a primitive one in the order, and has been lost in *Agnostus*, *Microdiscus*, *Ampyx*, and *Dionide*.

The ontogeny of higher genera shows that the true eyes and free cheeks are first developed ventrally, appearing later at the marginal, and then on the dorsal side of the cephalon. Therefore the *Agnostidae*, *Trinucleidae*, and *Harpedidae* have a very primitive head structure, characteristic of the early larval forms of higher families. Other secondary features show that this order, though the most primitive in many

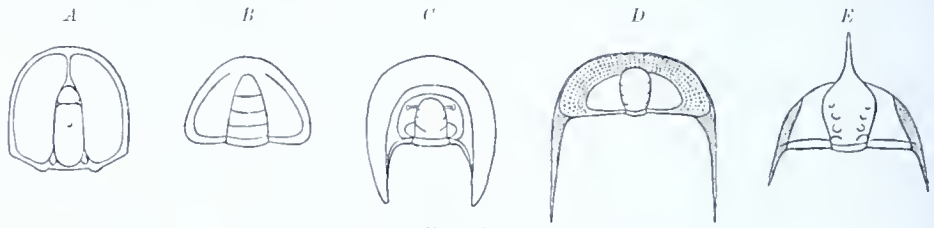


Fig. 1281.

Cephala of *Hypoparia*. *A*, *Agnostus*. *B*, *Microdiscus*. *C*, *Harpes*. *D*, *Trinucleus*. *E*, *Ampyx* (after Beecher).

respects, is more specialised than either of the others, except in their highest genera. The characters referred to are the glabella and pygidium. Very few species show the primitive segmentation of the glabella, it being usually smooth and inflated and resembling in its specialisation such higher genera as *Proëtus*, *Asaphus*, and *Lichas*. The pygidium often fails to indicate its true number of segments. Many species of *Agnostus* and *Microdiscus* show no segments either on the axis or limb of the pygidium. *Trinucleus* and others may have a numerously annulated axis and fewer grooves on the pleural portions. The number of appendages corresponds to the axial divisions. The multiplication of segments in the pygidium, and their consequent crowding, make them quite rudimentary.

Family 1. **Agnostidae**. Dahlman.

Small forms, having the cephalon and pygidium elongate, nearly equal, and similar in form and markings. Free cheeks ventral, continuous; suture marginal or ventral. Eyes wanting. Thorax composed of from two to four segments, with grooved pleura. Cambrian and Ordovician.

Fig. 1282.

Agnostus granulatus, Barr. Cambrian; Skrey, Bohemia. $^5/_1$ (after Barrande).

Fig. 1283.

Agnostus pisiformis, Linn. Cambrian; Andrarum, Sweden. Complete individual, and fragment of limestone with detached cephala and pygidia.

Some species have spines at the genal angles, corresponding to the interocular spines of *Holmia* and young *Elliptocephala*, and not to the spiniform projections of the free cheeks. From their abbreviated thorax, and progressive loss of annulations on the glabella and pygidial axis, they must also be considered as degraded. *Microdiscus*, the earliest genus, shows in some species the normal pentamerous glabella, and annulated pygidial axis, while the later genus *Agnostus* has lost the annulations of both axis and pygidium.

Agnostus, Brongn. (Figs. 1281, *A*-1283). Cephalon and pygidium without annulations on their axes; thoracic segments, two. Extraordinarily abundant in the Middle

and Upper Cambrian and Ordovician rocks of Bohemia, Scandinavia, Great Britain, Spain, and America.

Microdiscus, Emmons (Fig. 1281, *B*). Cephalon and pygidium often showing their segmented nature by annulations on their axes; thorax with three or four segments. Cambrian.

Family 2. **Harpedidae.** Barrande.

Cephalon large, with a broad marginal expansion or limb; glabella short and prominent. Free cheeks ventral, continuous; suture marginal, following the outer edge of limb. Paired simple eye-spots or ocelli, single or double, at the distal ends of well-marked eye-lines on the fixed cheeks, extending outward from the glabella. Thorax of from twenty-five to twenty-nine segments, with long grooved pleura. Pygidium (in Harpes) *very small, composed of but three or four segments.* Ordovician to Devonian.

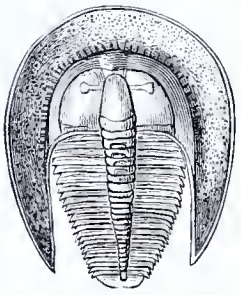


Fig. 1284.

Harpes ungula, Sternberg sp. Ordovician; Bohemia (after Barrande).

Harpes, in many respects, is one of the most interesting genera of Trilobites, being very unlike other forms. The broad hippocrepian pitted limb of the cephalon has its counterpart in *Trinucleus* and *Dionide*, although less well developed in these genera. The head is also relatively longer and larger, both features being decidedly larval. It is the only family known in which functional visual spots or ocelli are situated on the fixed cheeks. The young *Trinucleus* has similar ocelli. The great number of free segments in *Harpes* is another primitive character, and the cephalon still remains larger than the thorax and pygidium.

Harpes, Goldfuss (Figs. 1281, *C*, 1284). Principally Ordovician and Silurian, although a few Devonian forms are known.

Family 3. **Trinucleidae.** Barrande.

Cephalon larger than the thorax or pygidium; genal angles produced into spines. Free cheeks continuous, almost wholly ventral, carrying the genal spines; suture marginal or submarginal. Paired simple eyes or ocelli generally absent in adult forms; compound eyes wanting. Thoracic segments five or six, with grooved pleura. Pygidium triangular; margin entire; axis with a number of annulations; limb grooved. Ordovician and Silurian.

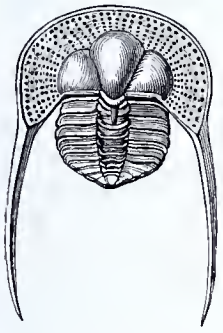


Fig. 1285.

Trinucleus Goldfussi, Barr. Ordovician (Et. D); Wesela, Bohemia. 1/1.

Fig. 1286.

Ampyx nasuta, Dalman. Ordovician; Pulkowa, Russia. 1/1.

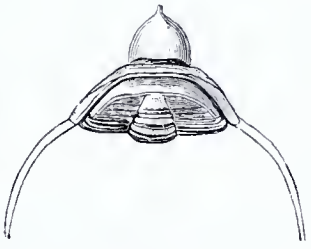


Fig. 1287.

Ampyx Portlocki, Barr. Ordovician (Et. D); Leiskov, Bohemia. 1/1 (after Barrande).

Trinucleus, Lhwyd (Figs. 1281, *D*, 1285). Cephalon with a broad, regularly pitted border, produced behind into long genal spines; glabella prominent; thorax of six segments; axis narrow; pygidium triangular, wide, short. Ordovician; Europe and North America.

Dionide, Barr. Like *Trinucleus*, but with irregularly punctate border, and larger pygidium. Ordovician; Europe.

Ampyx, Dalman (Figs. 1286, 1287). Thorax and pygidium resembling *Trinucleus*;

cephalon subtriangular, without pitted limb; glabella large, prominent, narrow behind and enlarged anteriorly, often produced into a frontal spine. Genal angles spiniform; thoracic segments five or six. Chiefly Ordovician, rare in Silurian; Europe and North America.

Order 2. OPISTHOPARIA. Beecher.

Free cheeks generally separate, always bearing the genal angles. Facial sutures extending forward from the posterior part of the cephalon within the genal angles, and cutting the anterior margin separately, or more rarely uniting in front of the glabella. Compound paired holochroal eyes on free cheeks, and well developed in all but the most primitive family.

The families which are here placed under this order lend themselves quite readily to an arrangement based upon the characters successively appearing in the ontogeny of any of the higher forms. Thus, *Sao*, *Ptychoparia*, and other genera of the *Olenidae* have first a protaspis stage only comparable in the structure of the cephalon with the genera of the preceding order. Therefore this stage does not enter into consideration

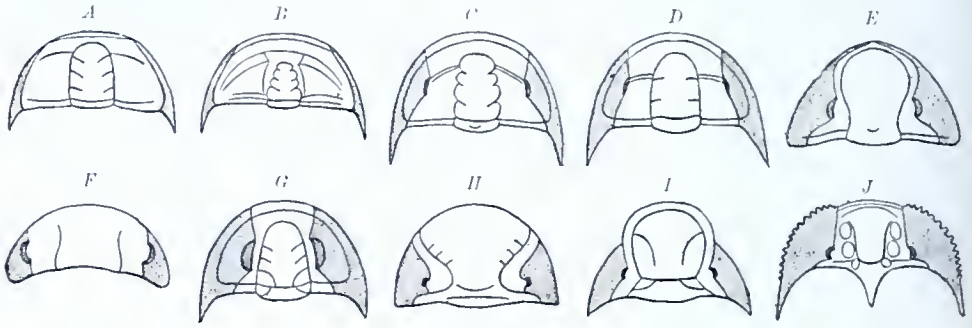


FIG. 1288.

Cephala of *Opisthoparia*. *A*, *Atops*. *B*, *Conocoryphe*. *C*, *Ptychoparia*. *D*, *Olenus*. *E*, *Asaphus*. *F*, *Illaenus*. *G*, *Proetus*. *H*, *Bronteus*. *I*, *Lichas*. *J*, *Acidaspis* (after Beecher).

in an arrangement of the families of the *Opisthoparia*. In the later stages, however, there is a direct agreement of structure with the lower genera of this order. The nepionic *Sao*, with two thoracic segments (Fig. 1279, *B*), has a head structure agreeing in essential features with that in *Atops* or *Conocoryphe* (Figs. 1288, *A*, *B*). A later nepionic stage, with eight thoracic segments (Fig. 1279, *C*) agrees closely with the adult *Ptychoparia* or *Olenus* (Figs. 1288, *C*, *D*). These facts clearly indicate that the family *Conocoryphidae* should be put at the base of this extensive order. Moreover, as *Ptychoparia* and *Olenus* are more primitive and simpler genera than *Sao*, they, as typifying the family *Olenidae*, govern its position, which accordingly would be next after the *Conocoryphidae*.

Variations in the position of the eyes, the relative size of the free and fixed cheeks, and the degree of specialisation of the glabella have a definite order in the ontogeny of any Trilobite, and furnish characters of taxonomic value in arranging the families placed under the *Opisthoparia* (see Fig. 1288).

Family 1. **Conocoryphidae**. Angelin.

Free cheeks very narrow, forming the lateral margins of the cephalon, and bearing the genal spines. Fixed cheeks large, usually traversed by an eye-line extending from near the anterior end of the glabella. Facial sutures running from just within the genal angles, curving forward, and cutting the anterior lateral margins of the cephalon. Eyes

rudimentary or absent. Thorax with from fourteen to seventeen segments. Pygidium small and of few segments. Cambrian.

The genera comprised under this family present a number of very primitive characters, such as are displayed only in the larval stages of higher forms. The free cheeks are narrow and marginal, and may be compared with those in the nepionic stages of *Sao* and *Ptychoparia*. Eyes have not been detected, but the presence of an eye-line suggests their possible existence. The variations in the glabella are very marked, and are as great as those which in higher forms attain some importance as family characteristics.

So far as known, all the larval forms in the other families of the *Opisthoparia* agree in having the narrow marginal free cheeks, bearing the genal angles. The eye-line is present in most of the adult *Olenidae*, and in the early stages of all so far as known, so that the general average of characters in the *Conocoryphidae* represents the main larval features throughout the other families.

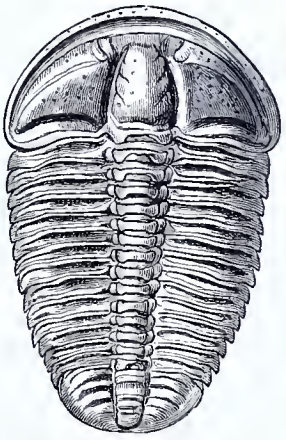


Fig. 1289.

Conocoryphe Sulzeri, Schloth. Without the free cheeks. Cambrian (Et. C); Ginetz, Bohemia. $^1/_1$.

Fig. 1290.

Cephalon of *Conocoryphe Sulzeri*, Schloth.

Fig. 1291.

Cephalon of *Atops trilineatus*, Emmons.

Conocoryphe, Corda (*Conocephalites*, Barr.), (Figs. 1289, 1290). Cephalon semicircular; genal angles produced into spines; glabella distinctly lobed, wide behind and contracted in front, not extending to the frontal border. Fixed cheeks very large, with conspicuous furrow parallel to the anterior margin; free cheeks narrow, marginal; thorax of fourteen segments Cambrian; Europe and North America.

Atops, Emmons (Fig. 1291). Differs from *Conocoryphe* in having a more cylindrical and longer glabella, small pygidium, and seventeen free segments. Lower Cambrian; North America.

Ctenocephalus, Corda. Like *Conocoryphe*, but with a lobe in front of the glabella, which is also less strongly defined; free cheeks larger; pygidium much smaller; free segments fifteen. Cambrian; Europe and North America.

Bathynotus, Hall. Differs from *Atops* and *Conocoryphe* in its wider axis; free cheeks united in front and extending backward into long genal spines; thoracic segments thirteen; pleura hastate. Lower Cambrian; North America.

Family 2. **Olenidae.** Salter.

Cephalon larger than the pygidium, usually wider than long; genal angles commonly produced into spines; free cheeks separate. Facial suture extending forward from the posterior margin of cephalon along the eye-lobes, and either cutting the anterior margin separately, or meeting on the median line. Eyes crescentic, reniform, or semicircular, situated at the ends of eye-lines in all but the highest genera. Trunk long, composed of from eight (?) to twenty-six free segments. Pygidium frequently small; margin entire or spinose. Principally Cambrian, but extending also into the Ordovician.

Paradoxides, Brongt. (Figs. 1292, 1293). Glabella enlarging in front, lobes defined; thorax with from seventeen to twenty free segments, pleura with spiniform or hastate extremities; pygidium a small plate-like termination of the axis, segmented. Individuals sometimes attaining a length of 0·6 m. or more. Very abundant in the Middle Cambrian of Europe, North America, and Australia.

Olenellus, Hall. Fourteen free segments; pygidium a long telson-like spine. Lower Cambrian: North America and Europe.

Holmia, Matthew (Fig. 1294). Sixteen free segments; pygidium a small plate without apparent segmented divisions. Lower Cambrian; Norway.

Remopleurides, Portlock (Fig. 1295). Glabella expanded; axis wide; free segments eleven to thirteen; pygidium small, axis often reduced to two annulations, the pleural portion produced behind into a flat expansion. Ordovician; Europe and North America.

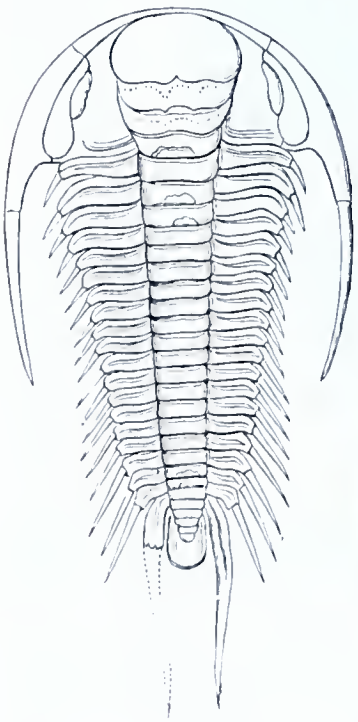


Fig. 1292.

Paradoxides Bohemicus, Barr. Cambrian (Et. C); Ginetz, Bohemia. 1/2.

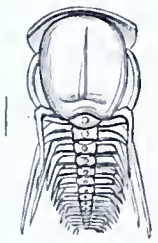


Fig. 1293.

Paradoxides (cf. young of *P. inflatus*, Corda sp. = *Hydrocephalus carens*, Barr.). Cambrian; Skrey, Bohemia.

Fig. 1295.

Remopleurides (*Caphyra*) *radians*, Barr. Ordovician (Et. D); Königshof, Bohemia. 1/1 (after Barrande).

Fig. 1294.

Holmia Kjerulfi, Linnarson. Cambrian; Ringsaker, Norway. Part of the glabella removed, exposing hypostoma beneath. 3/4 (after Holm).

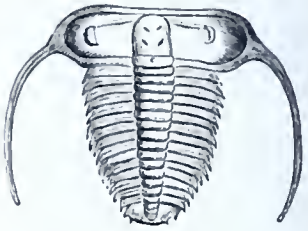


Fig. 1296.

Eurycare brevicauda, Ang. Cambrian; Andrarum, Sweden (after Angelin).

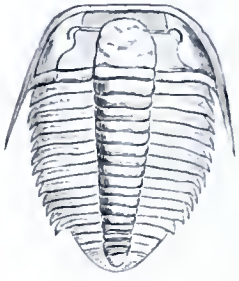


Fig. 1297.

Olenus truncatus, Brunn. Cambrian; Andrarum, Sweden (after Angelin).

Eurycare, Angelin (Fig. 1296). Cephalic shield short, posterior angles produced into long curved spines; thoracic segments seven to nine. Cambrian; Europe.

Olenus, Dalman (Fig. 1297). Glabella defined, not narrowing anteriorly; thoracic segments twelve to fifteen, pleura with sharp-pointed extremities, bent backwards; axis narrow, pygidium small. Cambrian and Ordovician; Europe.

Ptychoparia, Corda (Fig. 1288, *C*). Resembles *Olenus*, but with tapering glabella, wrinkled limb, and larger pygidium. Cambrian; Europe and North America.

Agraulus, Corda. Body elongate oval; cephalic shield large, paraboloid, limb broad; eyes small; thoracic segments sixteen; pygidium small, with rounded margin and three annulations in the axis. Cambrian; Europe and North America.

Ellipsocephalus, Zenker (Fig. 1298). Cephalic shield semicircular; glabella smooth, obtusely angular in front; free cheeks short and narrow; thoracic segments twelve to fourteen; pygidium short, rudimentary. Cambrian; Europe and North America.

Sao, Barr. (Figs. 1278, 1299). Glabella slightly tapering forwards, extending two-thirds the length of the cranidium, and having three pairs of distinct lateral furrows; thoracic segments seventeen; pygidium very small. Cambrian; Europe.

Triarthrus, Green (Figs. 1274, 1300). Glabella large and well-defined, furrows not continuous; thoracic segments fourteen to sixteen; pleura grooved; pygidium with six segments in the axis, margin entire. Ordovician; America and Scandinavia.

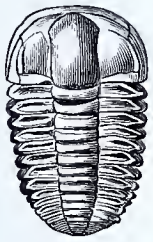


Fig. 1298.

Ellipsocephalus Hoffi, Schloth. Cambrian; Ginetz, Bohemia.

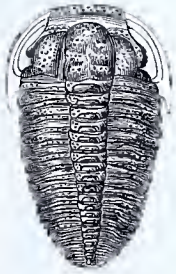


Fig. 1299.

Sao hirsuta, Barr. Cambrian; Skrey, Bohemia.

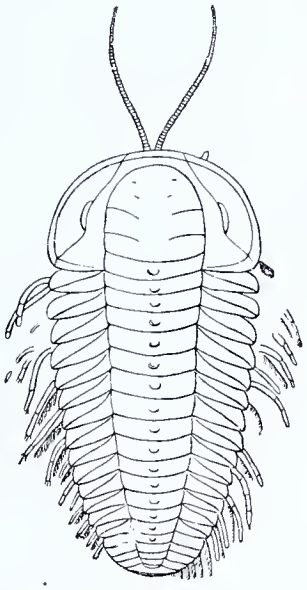


Fig. 1300.

Triarthrus Becki, Green. With antennae and legs. Ordovician; Rome, New York. $^5/_2$ (after Beecher).

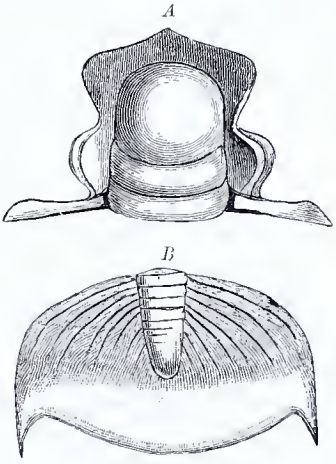


Fig. 1301.

Dikelocephalus Minnesotensis, D. Owen. Cambrian; Wisconsin. *A*, Cranidium. *B*, Pygidium (after Hall).

Dikelocephalus, Owen (Fig. 1301). Cephalon large, crescentic; glabella not extending to frontal margin; eyes well developed; thoracic segments nine. Pygidium very large, broad and fan-like, with the sides produced posteriorly into spines, axis with four to six rings, extending less than two-thirds the length of the pygidium. Cambrian; North America and Europe.

Family 3. **Asaphidae**. Emmrich.

Cephalon and pygidium well developed; glabella often obscurely limited. Free cheeks usually separate. Facial sutures extending forwards from the posterior edge of the cephalon within the genal angles, and cutting the lateral or anterior margins, occasionally uniting in front of the glabella. Eyes usually present, smooth, well developed, sometimes of very considerable size, even occupying the entire surface of the free cheeks. Thorax generally composed of eight or ten segments, but varying from five to ten. Pygidium large, often with wide doublure. Cambrian to Silurian.

Asaphus, Brongt. (*Cryptonymus*, Eichw.), (Figs. 1265, 1288, *C*, 1302). Cephalic and caudal shields of nearly equal size, with broad infolded margin; glabella expanded,

nearly smooth ; free cheeks large ; hypostoma deeply forked ; eyes large and prominent.;

Fig. 1302.

Asaphus expansus, Linn. Ordovician ; Pulkowa, near St. Petersburg, Russia (after Salter).

thoracic segments eight ; pygidium not strongly segmented, often nearly smooth. Some species attain a length of 0·6 m. Very profuse in the Ordovician of Europe and North America.

Sub-genus : *Megalaspis*, Angelin (Fig. 1303). Like *Asaphus*, but with more defined and cylindrical glabella. Ordovician ; Europe.

Ogygia, Brongt. (Fig. 1304). Glabella not greatly expanded, and with four or five lateral furrows ; hypostoma pentagonal, with rounded posterior margin ; thoracic segments with grooved pleura. Ordovician ; Europe.

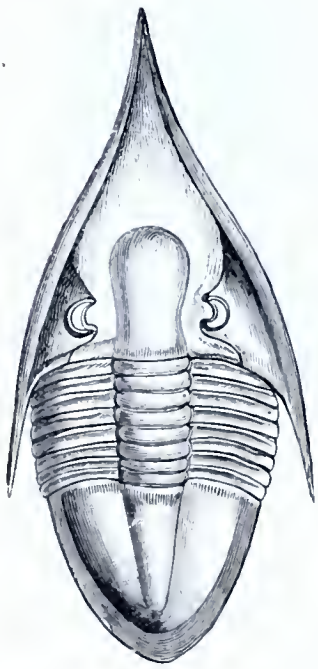


Fig. 1303.

Megalaspis extenuata, Ang. Ordovician ; East Gottland, Sweden. 1/1 (after Angelin).

Illaenus, Dalman (Figs. 1288, *F*, 1305). Cephalic and caudal shields large and convex, semicircular in outline ; glabella smooth, indistinct ; free cheeks small ; hypostoma convex, ovoid, posteriorly notched ; thoracic segments usually ten, with smooth pleura ; pygidium smooth, with short and inconspicuous axis. Abundant in the Ordovician and Silurian of Europe, Asia, and North America.

Nileus, Dalman. Thoracic segments eight ; axis very broad ; eyes large. Ordovician ; Europe.

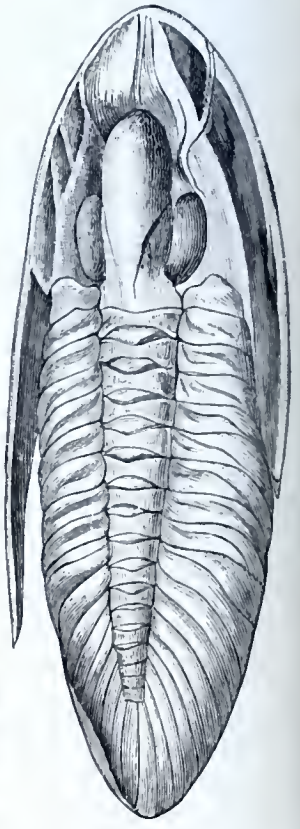


Fig. 1304.

Ogygia Guettardi, Brong. Ordovician ; Angers, France. Mechanically deformed individual (after Brongniart).

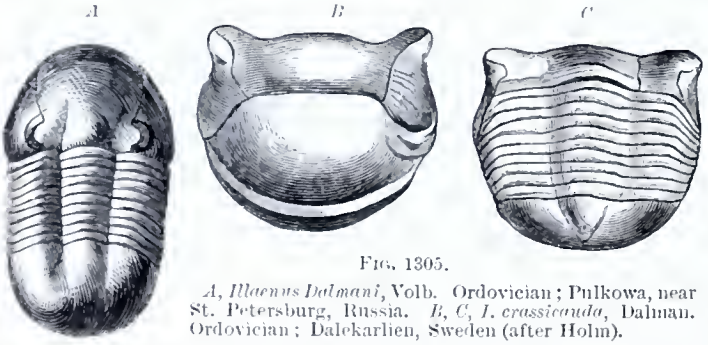


Fig. 1305.

A, *Illaenus Dalmani*, Volb. Ordovician ; Pulkowa, near St. Petersburg, Russia. *B*, *C*, *I. crassicauda*, Dalman. Ordovician ; Dalekarlien, Sweden (after Holm).

Aeglina, Barr. (Fig. 1306). Glabella strongly convex, prominent, smooth ; fixed

cheeks suppressed; eyes very large, occupying nearly the whole area of the free cheeks; thoracic segments five or six; pleura grooved; pygidium large, with short axis. Ordovician; Europe.

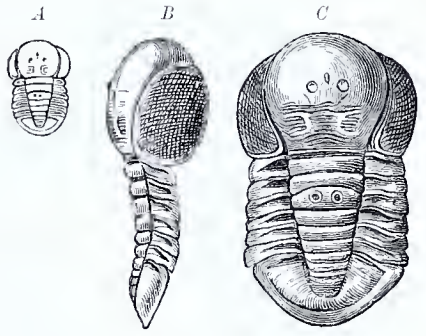


Fig. 1306.

Aeglina prisca, Barr. Ordovician (Et. D); Vosek, Bohemia. *A*, Nat. size. *B*, *C*, Enlarged (after Barrande).

Family 4. **Proëtidae**. Barrande.

Cephalon about one-third of the whole animal; genal angles generally produced into spines; glabella tumid, with two lateral basal lobes defined by oblique furrows in front of the neck segment. Free cheeks large, separate. Sutures extending from the posterior margin inward to the eyes, and then forward, cutting the anterior margin separately. Eyes usually prominent, often large. Thorax of from eight to twenty-two free segments, with grooved pleura. Pygidium usually of many segments; pleural and axial portions strongly grooved; margin entire or dentate. Ordovician to Permian.

Proëtus, Steininger (Figs. 1275, 1307). Head-shield semicircular, with thickened marginal rim; glabella well defined, extending nearly to the anterior margin, lateral furrows obsolescent, basal lobes often present. Eyes large, crescentic, near the glabella; thoracic segments usually ten, pleura grooved; pygidium semicircular, margin entire; axis elevated, segmented; limb ribbed. Ordovician to Carboniferous; common in the Devonian.

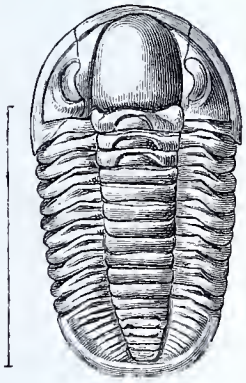


Fig. 1307.

Proëtus Bohemicus, Corda. Silurian (Et. E); Konieprus, Bohemia (after Barrande).

Phillipsia, Portlock (Fig. 1308). Like *Proëtus*, but with more prominent glabella, strong basal lobes, and larger, more segmented pygidium; thoracic segments nine. This genus replaces *Proëtus* in the later Palaeozoic horizons. The last surviving species occurs in the Permian of North America. Maximum development in Lower Carboniferous.

Fig. 1308.

Phillipsia gemmulifera, Phill. Carboniferous Limestone; Kildare, Ireland.

Fig. 1309.

Arethusina Koninecki, Barr. Ordovician (Et. D); Kuchelberg, near Prague. 1/1.

Arethusina, Barr. (Fig. 1309). Glabella about half the total length of head-shield, contracted toward the front, with oblique lateral furrows and basal lobes; fixed cheeks large; eyes small, situated at the ends of distinct eye-lines from the glabella; thorax with twenty-two short segments; pygidium small. This is the most primitive genus of the family, and the only one retaining archaic eye-lines. The eyes, too, are more distant and forward than in other genera, and the number of thoracic segments is larger. Ordovician; Europe.

Family 5. **Bronteidae**. Barrande.

Dorsal shield broadly elliptical. Cephalon less than one-third the entire length; glabella rapidly expanding in front, with faint indications of lobes. Free cheeks larger than the fixed. Facial sutures extending from the posterior margin just behind the eyes abruptly inward around the palpebral lobes, and then diverging and cutting the antero-

lateral margins separately. Eyes crescentic. Thorax of ten segments, with ridged pleura. Pygidium longer than cephalon or thorax; axis very short, with radiating furrows extending from it across the broad limb toward the margin: doublure very wide; margin generally entire. Ordovician to Devonian.

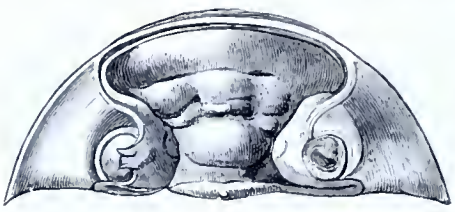


Fig. 1310.

Cephalon of *Bronteus palifer*, Beyr. Devonian (Et. F); Konieprus, Bohemia (after Barrande).

This comprises the single genus *Bronteus*, Goldfuss (Figs. 1264, 1288, *H*, 1310). Ordovician to Devonian; Europe and North America. Most abundant in the Silurian and Devonian of Bohemia.

Family 6. **Lichadidae.** Barrande.

Dorsal shield generally large and flat, with granulated test. Cephalon small, not more than one-fourth the entire length; genal angles spiniform. Free cheeks separate: sutures extending from the posterior margin obliquely inward to the eyes, and then almost directly forward, cutting the margin separately. Glabella broad, with a large, often tumid central lobe, and from one to three side lobes. Eyes not large. Thorax with nine or ten segments, and grooved and falcate pleura. Pygidium large, flat, commonly with toothed or notched margin corresponding to the pleural grooves; doublure very broad. Ordovician to Devonian.

Most of the forms of this family are above the average size of Trilobites, and several species are among the largest of the class. They are all thin-shelled, and so loosely articulated that entire specimens are extremely rare.

Lichas, Dalman s. str. (Figs. 1262, 1311). Anterior lobe of the glabella dominating the other lobes, and continuous with the axis: lateral lobes reniform and small. Ordovician and Silurian; Europe and North America.

Sub-genera: *Arges*, Goldf. (Fig. 1312). Lateral lobes of glabella strongly defined, nearly as large as the central one, and divided transversely by a furrow; lobes and neck ring often spiniferous; pygidium with dentate margin and spiniform pleural extensions. Silurian and Devonian.

Fig. 1311.

Lichas laciniatus, Wahlb. Silurian; Sweden (after Angelin).

Fig. 1312.

Arges armatus, Goldfuss. Devonian; Germany (after Beyrich).

Dicranogmus, Corda (Fig. 1313). Glabella divided by two longitudinal and one transverse furrow into angular lobes; pygidium with annulated axis; limb with a few short denticulations. Silurian.

Fig. 1313.

Dicranogmus plynnensis, Hall and Clarke. Silurian; New York.

Fig. 1314.

Conolichas Schmidti, Dames. Ordovician; Germany (after Dames)

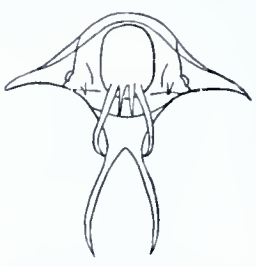


Fig. 1315.

Ceratolichas grypa, Hall and Clarke. Devonian; New York (after Hall and Clarke).

Conolichas, Dames (Fig. 1314). Glabella having one large protruding central, and two prominent lateral lobes, with sometimes two smaller basal lobes. Ordovician to Devonian.

Ceratolichas, Hall and Clarke (Fig. 1315*a*). Central lobe arched, tumid, with smaller side lobes; central lobe and occipital ring with long curved spines. Devonian; North America.

Family 7. **Acidaspidae.** Barrande.

Dorsal shield spinose. Cephalon transversely semi-elliptical, quadrate, or trapezoidal; genal angles spiniform. Glabella with one large median axial lobe and two or three lateral lobes. Free cheeks large, separate. Sutures extending from just within the genal angles abruptly inward to the eyes, and then forward, cutting the anterior margin each side of the glabella. Eyes small, often prominent. Thorax of eight to ten segments, with ridged pleura extended into hollow spines. Pygidium usually small, with spinous margin. Ordovician to Devonian.

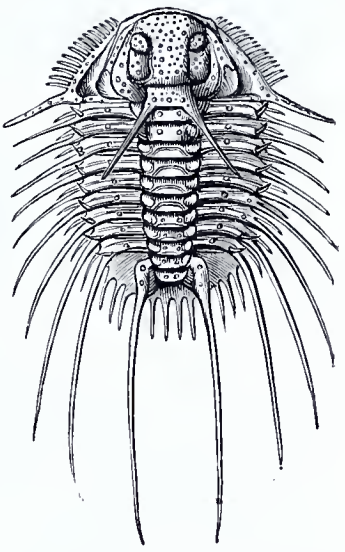


Fig. 1316.

Acidaspis Dufrenoyi, Barr. Silurian (Et. E); St. Iwan, Bohemia (after Barrande).

In this family, as well as in the *Lichadidae*, is to be found the highest expression of differentiation and specialisation among the *Opisthoparia*. The primitive pentamerous lobation of the axis of the cranidium is entirely obscured, and is only clearly seen in the protaspis and early nepionic stages. These two families are very closely related, the chief differences being noted in the size and character of the pygidium, and the ribbed or grooved pleura. The Lichades are generally much larger and flatter, but the smaller and spinose forms of *Arges* and *Ceratolichas* approach quite near some of the *Aeidaspidae*.

Aeidaspis, Murch. (Figs. 1276, 1288, *J*, 1316). Ordovician to Devonian; Europe and North America. *Dieranurus*, Conrad; *Aneyropyge*, Clarke; Devonian. *Selenopeltis*, Corda; Ordovician.

Order 3. PROPARIA. Beecher.

Free cheeks not bearing the genal angles. Facial sutures extending from the lateral margins of the cephalon in front of the genal angles, inward and forward, cutting the anterior margin separately or uniting in front of the glabella. Compound paired eyes scarcely developed or sometimes absent in the most primitive family; well developed and schizochroal in the highest family.

This is the only order of Trilobites which apparently begins during the known Palaeozoic, and unlike the other orders, had no pre-Cambrian existence. The earliest forms of the *Proparia* were initiated at the close of the Cambrian and dawn of the Ordovician. The greatest generic differentiation of the group was early attained; during the Silurian and Devonian a rapid decline ensued, and only one or two genera survived into the beginning of the Carboniferous.

Among the *Opisthoparia*, it was shown that the *Conocoryphidae* formed the natural base or most primitive family in the order, and was distinguished by the narrow marginal free cheeks and absence of well-developed eyes. It is of great interest and importance to be able to recognise in the *Proparia* a similar primitive family having characters in common with the other, but still clearly belonging to the higher order. *Plaeoparia*, *Areia*, and *Dindymene* of the *Encrinuridae* constitute a group of apparently blind Trilobites with narrow marginal free cheeks, and present in general the appearance of *Atops*, *Conocoryphe*, *Ctenocephalus*, etc., of the *Conocoryphidae*.

Family 1. **Encrinuridae.** Linnarsson.

Cephalon narrow, transverse. Fixed cheeks very large. Free cheeks long, narrow, separate, sometimes with a free rostral plate between the anterior extremities. Sutures extending from in front of the genal angles obliquely forward, and cutting the anterior margin in front of the glabella. Eyes very small or absent. Thorax of from nine to twelve segments, with ridged pleura. Pygidium generally composed of many segments; limb with strong ribs usually less in number than the annulations of the axis. Ordovician and Silurian.

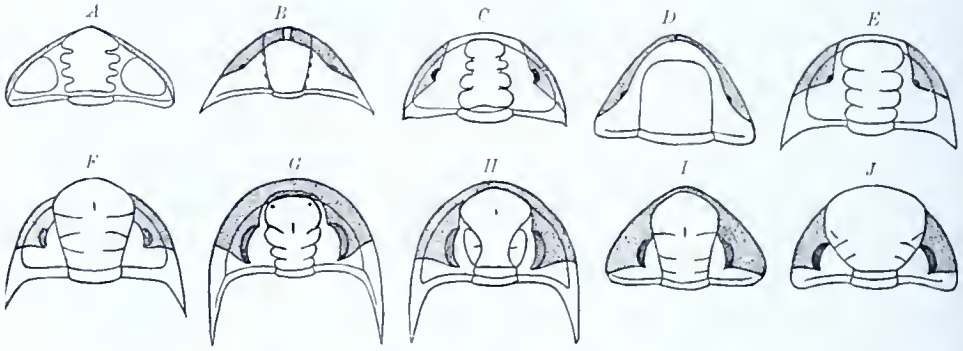


Fig. 1317.

Cephala of *Proparia*. *A*, *Placoparia*. *B*, *Encrinurus*. *C*, *Calymmene*. *D*, *Dipleura*. *E*, *Cheirurus* (*Ecoptochile*). *F*, *G*, *Dalmanites*. *H*, *Chasmops*. *I*, *Acaste*. *J*, *Phacops* (after Beecher).

Encrinurus, Emmrich (*Cromus*, Barr.), (Figs. 1262, 1317, *B*-1319). Cephalon tuberculated; glabella pyriform, prominent; free cheeks narrow, separated in front by a small rostral plate; eyes small, elevated on conical prominences; thoracic segments eleven; pygidium triangular, numerously segmented, limb with fewer ribs. Ordovician and Silurian; Europe and America.

Fig. 1318.

Encrinurus punctatus, Emmr. Silurian; Gottland.

Fig. 1319.

Encrinurus Bohemicus, Barr. Silurian (Et. E); Lochkow, Bohemia.

Placoparia, Corda (Fig. 1317, *A*). Glabella more strongly lobed than in *Encrinurus;* eyes obsolete; free cheeks long, narrow; thorax of twelve segments; pygidium small, with few segments. Ordovician; Europe.

Family 2. **Calymmenidae.** Brongniart.

Cephalon somewhat wider than long. Fixed cheeks large; genal angles rounded or produced into spines. Glabella narrowing anteriorly. Free cheeks long, separate, usually with a free plate between the anterior extremities. Sutures extending from just in front of the genal angles, converging anteriorly, and cutting the margins separately. Eyes small, facets numerous, visual surface seldom preserved. Thorax of thirteen segments, with grooved pleura. Pygidium of from six to fourteen segments; axis tapering. Ordovician to Devonian.

Fig. 1320.

Calymmene senaria, Conrad. Ordovician; Cincinnati, Ohio. 1/1.

Calymmene, Brongt. (Figs. 1317, *C*, 1320). Body oval in outline, possessing the power of enrolment to perfection; glabella conical, strongly convex, divided by three pairs of deep lateral grooves; eyes small; hypostoma quadrate, notched. Thorax of thirteen segments, axial furrows deep; pygidium of from six to

eleven segments, not distinctly marked off from the thorax. Ordovician and Silurian; Europe and North America; also Devonian of North America.

Homalonotus, Koenig (Fig. 1321). Body usually large, elongate, narrowing behind, indistinctly trilobed; glabella smooth, flattened and almost quadrate; pygidium elongate triangular, posterior margin rounded or pointed, axis with ten to fourteen annulations, sometimes smooth and without apparent segments. Ordovician to Devonian; Europe, America, and South Africa.

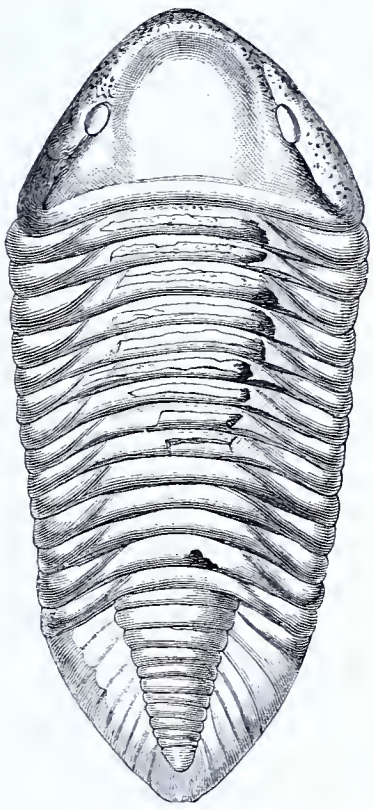


Fig. 1321.

Homalonotus (*Trimerus*) *delphinocephalus*, Green. Silurian; Lockport, New York.

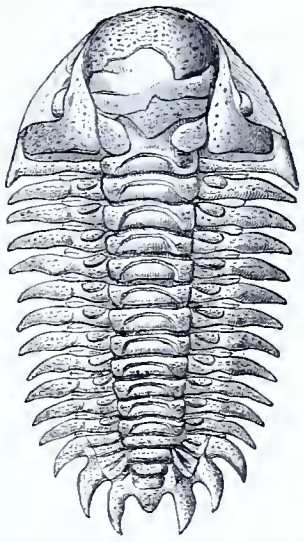


Fig. 1322.

Cheirurus insignis, Beyr. Silurian (Et. E); Kozolup, Bohemia. 1/1 (after Barrande).

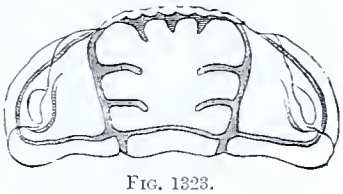


Fig. 1323.

Cephalon of *Amphion Fischeri*, Eichw. Ordovician: Pulkowa, Russia.

Family 3. **Cheiruridae.** Salter.

Glabella well defined. Free cheeks small, sometimes much reduced. Sutures extending from in front of the genal angles inward to the eyes, and then obliquely forward, cutting the anterior margin in front and on each side of the glabella. Eyes usually small. Thorax of from nine to eighteen segments, generally eleven; pleura often extended into hollow spines. Pygidium small, with from three to five segments; pleural elements commonly produced into spines. Principally Ordovician and Silurian, but extending into the Devonian.

Fig. 1324.

Sphaerexochus mirus, Beyr. Silurian; Listice, Bohemia. 1/1 (after Barrande).

Cheirurus, Beyr. (Figs. 1317, *E*, 1322). Glabella strongly convex and deeply grooved by three pairs of lateral furrows; thoracic segments eleven, more rarely nine to thirteen; pygidium with well-marked axis of four annulations, the pleura prolonged into points or spines. Species grouped into a number of sub-genera. Ordovician and Silurian; Europe and North America.

Amphion, Pander (Fig. 1323). Cephalon broad and short, with a distinct rim around the margin; glabella not strongly elevated, marked by two pairs of side furrows and short frontal furrows. Thoracic segments fifteen to eighteen with inflated pleura; pygidium smaller than cephalon, pleural ribs extended into spines. Commonly found in the enrolled condition. Ordovician; Europe and North America.

Sphaerexochus, Beyr. (Fig. 1324). Glabella ovoid or globular, with three pairs of

lateral furrows, the posterior one cutting off sub-circular basal lobes. Eyes small: thoracic segments ten, with smooth convex pleura; pygidium smaller than head-shield, composed of three segments, free at their ends. Ordovician and Silurian: Europe and North America.

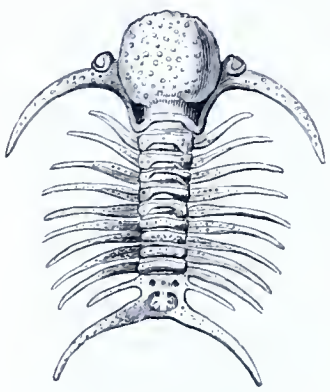


Fig. 1325.

Deiphon Forbesi, Barr. Silurian (Et. E); St. Iwan, Bohemia (after Barrande).

Deiphon, Barr. (Fig. 1325). Glabella globular, without lateral furrows; free cheeks minute; fixed cheeks produced at either side into a long curved spine. Eyes small, situated at the base of the spiniform fixed cheeks; thoracic segments nine, with free spiniform pleura; pygidium short, giving off two pairs of curved spinous processes. Silurian; Europe.

Family 4. **Phacopidae.** Salter.

Glabella tumid, widest in front. Free cheeks continuous, united anteriorly. Suture extending from in front of the genal angles inward to the eyes, and thence forward around the glabella. Eyes generally large, always with distinct facets, schizochroal. Thorax of eleven segments, with grooved pleura. Pygidium usually large and of many segments; limb ribbed; margin entire or dentate. Ordovician to Devonian.

Fig. 1327.

Phacops latifrons, Bronn. Devonian; Gerolstein, Eifel District.

Phacops, Emmrich (Figs. 1317, *J*, 1326, 1327). Glabella very wide and rounded in front, the two anterior pairs of lateral furrows inconspicuous or obsolete; genal angles short, generally rounded; eyes large, prominent; pleura rounded; pygidium semicircular, margin entire. Silurian to Upper Devonian; Europe and America.

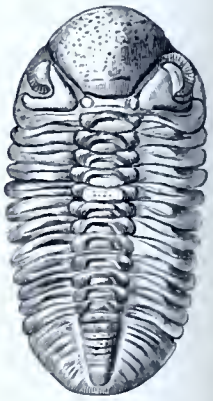


Fig. 1326.

Phacops Sternbergi, Barr. Devonian (Et. G); Hostin, Bohemia (after Barrande).

Trimerocephalus, M'Coy. Glabella tumid in front, lateral furrows faint or wanting except the basal one; fixed cheeks large; free cheeks forming a narrow anterior rim; eyes small, with a few large facets; pygidium small. Silurian and Devonian; Europe.

Fig. 1328.

Pterygometopus scleops, Dalm. Ordovician; Iswos, Esthonia (after Schmidt).

Fig. 1329.

Acaste Downingiae, Murch. Silurian; Ludlow, England (after Salter).

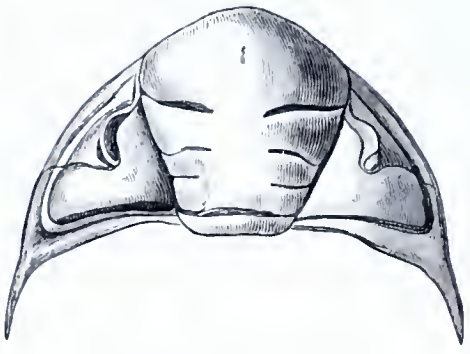


Fig. 1330.

Dalmanites socialis, Barr. Ordovician (Et. D); Wesela, near Prague, Bohemia. Cephalon, 1/1.

Pterygometopus, Schmidt (Fig. 1328). Cephalon obtusely angular in front; glabella enlarging anteriorly, lateral furrows well defined; pygidium as in *Phacops*. Ordovician; Europe and North America.

Acaste, Goldf. (Figs. 1317, *J*, 1329). Glabella slightly enlarging, with distinct lateral furrows; pygidium often

pointed, and usually with more segments than in *Phacops*. Ordovician and Silurian; Europe.

Dalmanites, Emmrich (Figs. 1261, 1317, *F*, *G*, 1330, 1331). Glabella with three well-marked lateral furrows; genal angles produced into spines; eyes large, prominent, and with many distinct facets; pygidium triangular, frequently pointed or mucronated, with more than eleven segments, sometimes twenty or more. Ordovician to Devonian; Europe, America, and East India.

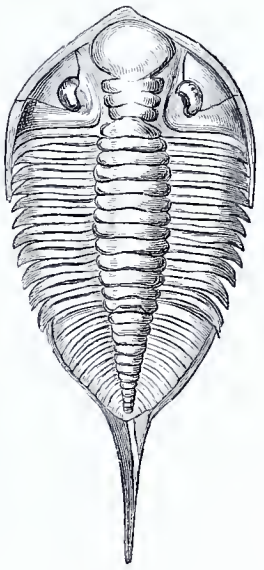


Fig. 1331.

Dalmanites limulurus, Green. Silurian; Lockport, New York (after Hall).

Chasmops, M'Coy (Fig. 1317, *H*). Differs from *Dalmanites* in having the second pair of glabellar lobes nearly separated from the axis, in the obsolescence of the third pair of lobes, and in its rounded pygidium. Ordovician; Europe.

Vertical Range and Distribution of Trilobites.

Trilobites are the only large division of the *Arthropoda* which has become extinct. Even in the earliest Cambrian they bear evidence of great antiquity,—in their diversified form, larval modifications, polymerous head, and caudal shields. These features show that Trilobite phylogeny must extend far back into pre-Cambrian times.

The maximum development of Trilobites occurred in the Cambrian and Ordovician, after which they steadily waned both in numbers and variety. The genera of the *Conocoryphidae* are wholly restricted to the Cambrian, and here also are found nearly all the *Olenidae* and *Agnostidae*, only scattering representatives of which survive into the Ordovician. The *Asaphidae* are the sole remaining family found in the Cambrian, and they are more characteristic of the Ordovician and Silurian.

All families of Trilobites are present in the Ordovician, and continue into the Silurian, with the exception of the *Conocoryphidae*, *Agnostidae*, and *Olenidae*, which are properly Cambrian types. The Devonian witnesses a decline in the number of families present, and with the close of this era, the class practically became extinct, since only five genera of one family, the *Proëtidae*, are met with in the Carboniferous, and the single genus *Phillipsia* alone persists as late as the Permian.

As regards their geographical distribution, some genera are of cosmopolitan occurrence: such as *Agnostus*, *Conocoryphe*, *Ptychoparia*, *Paradoxides*, *Trinucleus*, *Asaphus*, *Illaenus*, *Proëtus*, *Phillipsia*, *Acidaspis*, *Lichas*, *Calymmene*, *Homalonotus*, *Cheirurus*, *Phacops*, *Dalmanites*, and others. The majority of forms, however, are extremely limited in distribution, so that a large number of genera found in Sweden, Bohemia, England, and North America are unknown outside of certain very restricted areas; and the total number of species common to both sides of the Atlantic is very small.

A remarkable contrast is observable between the older Palaeozoic Trilobites of the northern parts of Europe, and those of the middle and southern portions. While the majority of northern genera and species are common to Great Britain, Scandinavia, and Russia, the forms of the central European provinces (Bohemia, Thuringia, Fichtelberg, the Hartz, Belgium, Brittany, Northern Spain, Portugal, the Pyrenees, the Alps, and Sardinia) are so dissimilar as to stand in closer relationships with the North American than with the first-named Trilobite fauna. Of the 350 species found in Norway and Sweden, and of the 275 in Bohemia, only six are common to both provinces, and it is doubtful if these are really identical.

The first of the accompanying tables shows the range and relative development of the orders and the class; the second represents the vertical range of the several families of Trilobites.

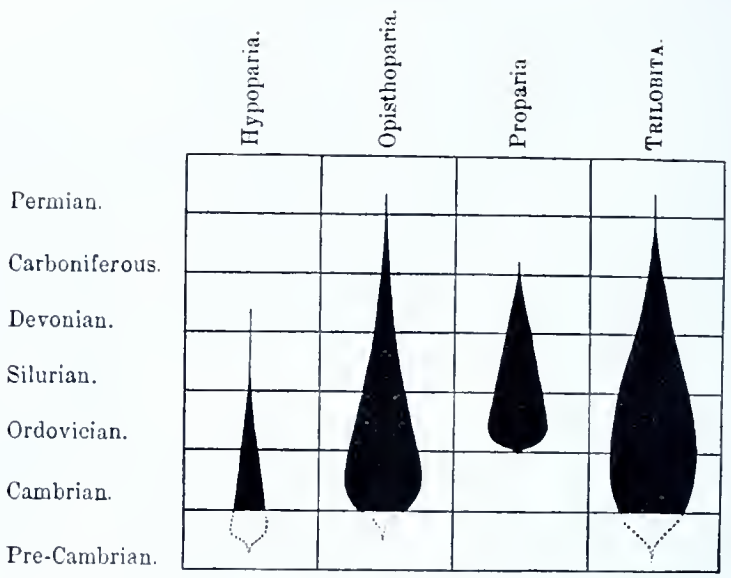


TABLE SHOWING VERTICAL RANGE OF TRILOBITES.

Families.	Cambrian.	Ordovician.	Silurian.	Devonian.	Carboniferous.	Permian.
Order 1. Hypoparia						
Family 1. Agnostidae	—	—				
2. Harpedidae		—	—	—		
3. Trinucleidae		—	—			
Order 2. Opisthoparia						
Family 1. Conocoryphidae	—					
2. Olenidae	—	—				
3. Asaphidae		—	—			
4. Proëtidae		—	—	—	—	—
5. Bronteidae		—	—	—		
6. Lichadidae		—	—	—		
7. Aeidaspidae		—	—	—		
Order 3. Proparia						
Family 1. Encrinuridae		—	—			
2. Calymmenidae		—	—	—		
3. Cheiruridae		—	—	—		
4. Phacopidae		—	—	—		
Total Number of Families	4	13	11	8	1	1

[The foregoing chapter on the **Trilobita** has been abbreviated from an essay prepared expressly for this work by our foremost authority on the group, Professor Charles E. Beecher of Yale University, New Haven. About a score of new figures have also been introdueed in the text, borrowed mainly from Dr. Beecher's original contributions. These last should be consulted by every student in conneetion with the present chapter.—Trans.]

Sub-Class B. EUCRUSTACEA. Kingsley. (Crustacea proper.)

Crustacea not having the body divided into median and lateral lobes; with filiform, plumose, or lamellate gills in either thoracic or abdominal region; with two pairs of antennae, and with the maxillae and mandibles never pediform. Nauplius stage either free-swimming or passed in the egg.

In the *Crustacea* proper the appendages of the cephalothorax are as follows: The first and second pairs are preoral and are known as the *antennae;* the third pair, placed at either side of the mouth, are the *mandibles;* the fourth and fifth pairs are secondary jaws, called *maxillae.* The appendages behind these vary in character, some being walking feet, while from one to three pairs may be subsidiary to the maxillae in eating, in which case they are called *maxillipeds.*

The *Eucrustacea* are commonly divided into *Entomostraca* and *Malacostraca,* but the first of these groups is not a homogeneous assemblage; it is rather a division in which have been placed all forms not members of the *Malacostraca,* the almost universal presence of a nauplius stage being its chief differential character. The *Eucrustacea* are here divided into the super-orders *Phyllopoda, Ostracoda, Copepoda, Cirripedia,* and *Malacostraca.*

Super-Order 1. PHYLLOPODA. Latreille.[1]

Eucrustacea of elongated form, often with distinctly segmented bodies, usually with flat shield-shaped or laterally compressed carapace.

Under the Phyllopods are embraced very differently formed Crustaceans of large and small size, living mostly in fresh water or salt marshes, and possessing in common little else than the leaf-like form of leg and a uniform developmental history. The segmentation of the body in higher forms (*Branchiopoda*) is very distinct, but in the water-fleas (*Cladocera*) it is usually quite incomplete. The number of body segments varies considerably among different genera. In the strongly segmented forms the body is elongated and protected in front by a flat or shield-shaped dorsal carapace (*Apus*), or it is naked (*Branchipus*). In the *Cladocera* and *Estheriidae,* which are enclosed in a bivalve shell, the body is laterally compressed, shortened, and indistinctly segmented. The line of division between thorax and abdomen

[1] Literature: A. Recent Forms.

Grube, E., Bemerkungen über die Phyllopoden, etc. (Wiegmann's Archiv für Naturgesch., XIX., XXXI.), 1853-65.—*Claus, C.,* Papers on Branchipus, Apus, and Limulus in Abhandl. Gesellsch. Wissensch. Göttingen, XVIII., 1873; and Arbeit. Zool. Inst. Wien., VI., 1886.—*Weismann, F. L. A.,* Zur Naturgeschichte der Daphniden (Zeitschr. Wissensch. Zool., XXVII., XXXIII.), 1876-80.—*Lankester, E. R.,* Several papers on Limulus, Apus, etc., in Quart. Journ. Microsc. Soc., XXI., 1881.—*Paekard, A. S.,* Monograph of the Phyllopod Crustacea of North America (12th Ann. Rept. U.S. Geogr. and Geol. Surv. Terr.), 1883.—*Hansen, H. J.,* Phyllopoda and Cirripedia. Plankton Expedition, 1895.

B. Fossil Forms.

Jones, T. R., On Fossil Estheriae and their Distribution (Quar. Journ. Geol. Soc., XIX.), 1863.—Monograph of the Fossil Estheriae (Palaeontogr. Soc.), 1862.—5th and 7th Repts. Comm. British Assoc. Adv. Sci. on Fossil Phyllopoda, 1887-89.—Geol. Mag. Sept. 1890, Feb. 1891, Dec. 1893, July 1894.—Trans. Geol. Soc. Glasgow, IX., 1890.—*Clarke, J. M.,* New Devonian Phyllopods (Amer. Journ. Sci., XXIII.), 1882.—*Hall, J.,* and *Clarke, J. M.,* Palaeontology of New York, VII., p. 206, 1888.—*Bernard, H. M.,* Fossil Apodidae (Nat. Sci., XI.), 1897.—*Schuchert, C.,* On the fossil Phyllopod genera Dipeltis and Protocaris (Proc. U. S. Nat. Mus. XIX.), 1897.

is seldom well defined; but, on the other hand, the head is sharply demarcated from the rest of the body, and is usually provided with two pairs of antennae and two large eyes, in addition to which there is often a small unpaired eye. About the mouth are the large upper lip (*hypostoma*), two broad cornute mandibles without palps, one or two pairs of maxillae, and often a lower lip in the form of two elevations below the mandible.

To the thorax are attached foliaceous, overlapping, biramous legs; these usually occur in considerable numbers, and while rarely more than eight pairs, they may vary from four to forty, and become smaller posteriorly. They serve for swimming and grasping, and as a rule are supplied at the base with respiratory tubes. The abdomen is partly without legs and frequently ends in a segment bent down or recurved, and furnished with two claw-shaped or expanded caudal appendages. All Phyllopods have the sexes distinct. The males are usually much less numerous than the females, and the latter produce chiefly by parthenogenesis.

Order 1. BRANCHIOPODA. Latreille.

Ten to forty or more pairs of leaf-like feet; carapace, when present, shield-shaped or bivalved; in the latter case enclosing the whole body and capable of being closed by a transverse adductor muscle.

Recent Branchiopods are almost exclusively inhabitants of fresh or brackish water, the exceptions being found in strong brine, as in Great Salt Lake, etc. The males are usually less numerous than the females, and in the case of some species several years may pass without their appearance, the females reproducing parthenogenetically.

Family 1. Limnadiidae. Baird.

Carapace bivalved, containing the whole body, and closed by a transverse adductor muscle. Antennae well developed; eyes sessile; thoracic legs in ten to twenty-eight pairs, the first one or two pairs in the male forming clasping organs. Abdomen small, without appendages, and terminated by a pair of caudal processes.

Estheria, Rüppel (Figs. 1332, 1333). Shell composed of two thin rounded valves,

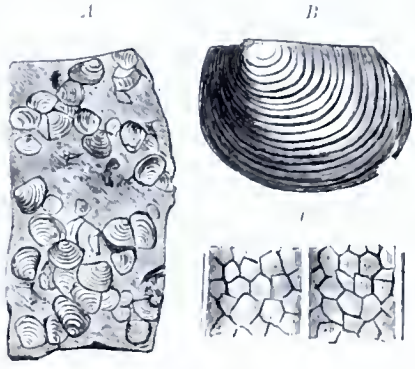


Fig. 1332.

Estheria minuta, Alberti. Lettenkohle Dolomite; Sinsheim, Baden. *A*, 1/1. *B*, 6/1. *C*. Portion of the exterior, 50/1.

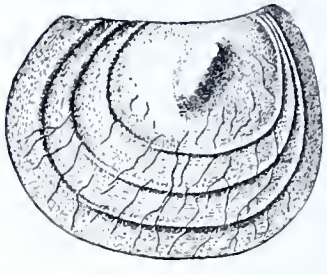


Fig. 1333.

Estheria, sp. indet. Lower barren Coal Measures; Carrollton, Ohio. Umbonal portion showing muscular or nuclear node, 13/1.

united by a straight toothless margin. External surface concentrically ridged or striated, and between the ridges are more or less regularly interlacing or branching

striae. The latter character serves to distinguish this genus from *Posidonomya* (p. 371). The beaks are not sharply defined, and the primitive portions sometimes bear a strong ocular or muscular node.

This genus has numerous fossil representatives, being first met with in the Devonian, and occurring mostly in brackish and shore deposits. It abounds in the productive Coal Measures, in the Permian, Trias (Lettenkohlenmergel), and Wealden, and has been found in the Pleistocene Clays of Canada.

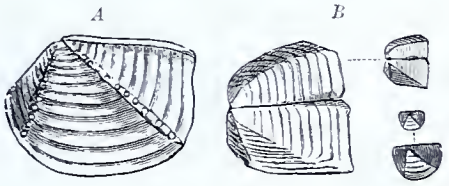


Fig. 1334.

A, *Leaia Leidyi*, Jones. Coal Measures; Pottsville, Pennsylvania. *B*, *L. Baentschiana*, Geinitz. Coal Measures; Neunkirchen, near Saarbrücken (after Goldenberg).

Fig. 1335.

Schizodiscus capsa, Clarke. Hamilton; Centerfield, New York. 2/1.

Leaia, Jones (Fig. 1334). Carapace marked by one or two diagonal ridges which run from the anterior end of the dorsal margin toward the lower margin. Carboniferous; Europe and North America.

Estheriella, Weiss. Carapace as in *Estheria*, but with radial riblets crossing the concentric striae. Permian; Russia. Buntersandstein; Saxony.

Schizodiscus, Clarke (Fig. 1335). Carapace peltate, with a straight hinge which is in the major axis of the shield. Each valve nearly a semicircle; surface marked with concentric ridges. Middle Devonian; New York.

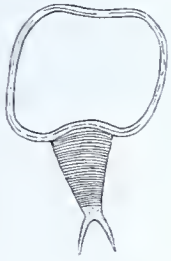


Fig. 1336.

Protocaris Marshi, Walcott. Cambrian; Georgia, Vermont. 2/3.

Family 2. **Apodidae.** Burmeister.

Eyes sessile and head with a large shield-like carapace extending over the thoracic segments; antennulae large and triflagellate; antennae greatly reduced except in the larva. Thorax with thirty to forty pairs of foliaceous feet; segmented abdomen without appendages save a pair of caudal filaments.

Protocaris, Walcott (Fig. 1336). The oldest representative of the *Apus*-type, and exhibits a remarkable similarity to *Apus* in its univalve carapace, multi-segmented abdomen, and single pair of caudal spines. Lower Cambrian; Vermont.

Apus, Schäff. (*Lepidurus*, Leach). Characters of the family. Trias to Recent.

Family 3. **Branchiopodidae.** Baird.

Head distinct, eyes stalked; carapace wanting. Thorax with eleven to nineteen pairs of foliaceous feet; abdomen terminating in two caudal processes.

Branchipodites, Woodward. Similar to the recent *Branchipus*. Oligocene of Bembridge, Isle of Wight. (*B. vectensis*, Woodw.)

Anomalocaris, Whiteaves. This name has been applied to bodies from the Cambrian of British Columbia which resemble the segmented abdomen of a Branchiopod, each segment bearing a pair of lamellate appendages. Although the objects abound where found, nothing is known of the carapace, nor is there any evidence of the surface markings which characterise most Crustacean shields. Its affinities are doubtful.

Order 2. CLADOCERA. Milne-Edwards.

Phyllopods with bivalve shell which partially or entirely encloses the body; antennae large, forming swimming organs; four pairs of leaf-like thoracic feet.

These have not yet been recognised with certainty in the fossil state. Possibly, however, *Lynceites ornatus*, Goldenberg, from the Carboniferous, belongs here.

Super-Order 2. COPEPODA. Latreille.

Body elongate, usually distinctly segmented, the anterior somites being fused, the posterior thoracic ones free. Both pairs of antennae well developed; four or five pairs of biramous thoracic feet. Abdomen short or long, without appendages except for a long caudal pair.

The *Copepoda* are without representatives in the fossil state.

Super-Order 3. OSTRACODA. Latreille.[1]

Small, indistinctly segmented Crustacea completely enclosed in a horny or calcareous bivalve shell. Only seven pairs of appendages present—two of antennae, one of mandibles, two of maxillae, and two pairs of thoracic feet. Abdomen short and rudimentary.

As a rule only the bivalve shell of the *Ostracoda* is found fossil, and since the classification is based principally upon characters presented by the appendages, the relations of recent to fossil forms cannot be made out with certainty, especially as the form and ornamentation of the shell are largely independent of the internal organisation.

The valves are closed by a sub-central adductor muscle, the attachment of which is marked on their inner sides by a tubercle, pit, or a number of small spots. The shell is compact in structure, commonly from 1 mm. to 4 mm. in length, although sometimes exceeding 20 mm. The outer surface may be

[1] Literature:

Bosquet, J., Description des Entomostracés fossiles de la craie de Maestricht (Mém. Soc. Roy. Sci. Liège, IV.), 1847.—Description des Entomostracés fossiles des terrains tertiaires de la France et de la Belgique (Mém. Couronn. Acad. Roy. Belg., XXIV.), 1850.—Monographie des Crustacés fossiles du terrain crétacé du Duche de Limburg (Mém. Commiss. Carte géol. Néerlande). Haarlem, 1854.—*Reuss, A. E.*, Die fossilen Entomostraceen des österreichen Tertiärbeckens (Haid. naturw. Abhandl., III.-Pt. 1), 1850.—Die Foraminiferen und Entomostraceen des Kreidemergels von Lemberg (*ibid.* IV., Pt. 1), 1851.—*Jones, T. R.*, A Monograph of the Entomostraca of the Cretaceous Formation of England (Palaeont. Soc.), 1849.—*Idem*, and *Hinde, G. J.*, A Supplemental Monograph of the Cretaceous Entomostraca of England and Ireland (*ibid.*), 1890.—*Jones, T. R.*, A Monograph of the Tertiary Entomostraca of England (*ibid.*), 1857.—*Idem*, and *Sherborn, C. D.*, A Supplemental Monograph of the Tertiary Entomostraca of England (*ibid.*), 1889.—*Jones, T. R.*, and *Kirkby, J. W.*, Notes on Palaeozoic bivalved Entomostraca, Nos. 1-32 (Ann. Mag. Nat. Hist.), 1855-95.—*Egger, O.*, Die Ostracoden der Miocänschichten bei Ortenburg (Neues Jahrb. p. 403), 1858.—*Speyer, O. W. C.*, Die fossilen Ostracoden aus den Casseler Tertiärbildungen (Cassel Jahresber., vol. XIII.), 1863.—*Brady, G. S., Crosskey, H. W.*, and *Robertson, D.*, A Monograph of the Post-Tertiary Entomostraca of Scotland (Palaeont. Soc.), 1874.—*Jones, T. R., Kirkby, J. W.*, and *Brady, G. S.*, A Monograph of the British Fossil bivalved Entomostraca from the Carboniferous Formations (*ibid.*), 1874, 1884.—*Jones, T. A.*, and *Holl, H. B.*, Notes on Palaeozoic bivalved Entomostraca (Ann. Mag. Nat. Hist. [4], III.), 1869.—*Brady, G. S.*, and *Norman, A. M.*, A Monograph of the marine and fresh-water Ostracoda of the North Atlantic, etc. (Sci. Trans. Roy. Dublin Soc., IV., V.), 1889-96.—*Lienenklaus, E.*, Monographie der Ostracoden des nordwestdeutschen Tertiärs (Zeitschr. deutsch. geol. Ges., XLVI.), 1894.—*Jones, T. R.*, and *Kirkby, J. W.*, On Carboniferous Ostracoda from Ireland (Sci. Trans. Roy. Dublin Soc., VI.), 1896.—*Ulrich, E. O.*, The Lower Silurian Ostracoda of Minnesota (Geol. Minn., III. Pt. 2, Palaeont.), 1897.—*Sherborn, C. D.*, The literature of fossil Ostracods (Nat. Sci. X.), 1897.

smooth and glossy, or granulose, pitted, reticulose, striate, hirsute, or otherwise marked, the effect being often quite ornamental. The two valves may be of equal size (*Beyrichia*), or more or less unequal, with either the right or left valve overlapping at the ventral border only (*Leperditia*), or at the dorsal border as well (*Bairdia*), or in some cases overlapping all round (*Cytherella*).

Most commonly the outline is ovate or reniform; in many cases, however, one or both ends may be pointed or drawn out in the form of a beak; and when the dorsum is straight, the ends may join it angularly. Although usually convex, the ventral margin is sometimes straight or gently concave. It is sometimes impossible to distinguish between anterior and posterior extremities, but as a rule the posterior half is somewhat thicker than the other, even though of equal or of lesser height. The hinge line may be straight or arcuate, the hinge itself being generally simple, although among the *Cytheridae* hinge teeth and corresponding sockets are often developed. There are commonly a small median and two larger lateral eyes; the position of the latter being often indicated on the exterior of the valves by a small "eye tubercle," or ocular spot.

Save for one or two families (*Cypridae*), Ostracods are almost wholly restricted to marine or brackish water. They are gregarious, and occur in vast hordes swimming near the surface or creeping over the bottom, preferring usually shallow depths. Their remains abound in nearly all the leading formations, and are often important rock-builders. The identification of fossil Ostracods is very difficult on account of their similarity of form and ornamentation, and usually minute size; and they cannot be well intercalated among the recent series for reasons already given. An arrangement of the families into higher groups is not attempted here, and only the more representative genera can be noticed.

Family 1. **Leperditiidae.** Jones.

Thick-shelled Ostracoda, mostly of considerable size. Valves smooth and glossy, of very compact structure, and in general regularly convex; hinge line straight; anterior and posterior ends obliquely truncated or rounded, and neither gaping nor excised.

Leperditia, Rouault (Fig. 1337). Shell sub-oblong with an oblique backward swing, from 2 mm. to 22 mm. long; dorsal edge straight, generally angular at the extremities; ventral outline rounded. Valves unequal, the right larger and overlapping ventral edge of the left. Surface often corneous in appearance, smooth, and eye tubercle generally present on the antero-dorsal quarter. A large rounded sub-central muscular imprint present on interior. Ordovician to Carboniferous.

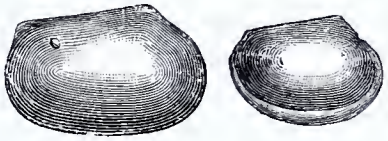


Fig. 1337.

Leperditia Hisingeri, Schmidt. Silurian; Wisby, Gottland. 1/1.

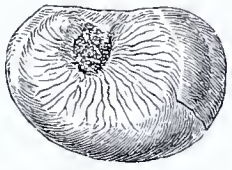


Fig. 1338.

Isochilina gigantea, Roemer. Silurian erratic; Lyck, East Prussia. 2/3 (after F. Roemer).

Leperditella, Ulrich. Similar to above, but the left instead of right valve is the larger, and has a groove within its ventral border for receiving simple edge of the right. Eye tubercle wanting. Length 1 mm. to 3 mm. Ordovician.

Isochilina, Jones (Fig. 1338). Like *Leperditia* except that the valves do not overlap but are equal in every respect. Ordovician and Silurian.

Aparchites, Jones. Shell not over 3 mm. in length, equivalve, sub-ovate or oblong; ventral edge thickened, often bevelled. Ordovician and Silurian.

Family 2. **Beyrichiidae.** Jones.

Small equivalve Ostracoda with a long straight hinge. Shells vertically sulcated and more or less lobate, varying from forms having a simple median depression to others in which the surface of the valves is raised into numerous low lobes, ridges or nodes.

Primitia, Jones and Holl (Fig. 1339). Valves ovate or oblong, ventral margin rounded, not over 2 mm. long. Well-marked sub-central pit or sulcus, with furrow extending to hinge line. Cambrian to Carboniferous.

Fig. 1339.

Primitia prunella, Barr. Silurian (E); Königshof, Bohemia (after Barrande).

Dicranella, Ulrich. Differs from *Primitia* in having long horn-like diverging prominences on one or both sides of the central sulcus. Ordovician.

Aechmina, Jones and Holl. Like *Primitia*, but having instead of the sulcus a single, sometimes enormously developed horn-like process. Ordovician to Devonian.

Eurychilina, Ulrich. Oblong or semi-elliptical shells having a sub-central Primitian sulcus, the posterior edge of which is often raised in to a small rounded node. Anterior, ventral, and posterior margins provided with a wide, often radially marked frill-like border. Ordovician.

Kloedinia, Jones and Holl. Intermediate between *Primitia* and *Beyrichia*. Its more or less well-defined small lobe between the two sulci represents the median lobe of *Beyrichia*. Ordovician to Devonian.

Beyrichia, M'Coy (Figs. 1340, 1341). Typically the valves have three lobes or nodes, of which the central one is the smallest, and commonly quite isolated from the other two. The outer ones are sometimes connected ventrally, and are not infrequently broken up into sets of smaller nodes; occasionally all of them are united below. Ordovician to Carboniferous.

Fig. 1340.

Beyrichia tuberculata, Klöden. Silurian erratic; Brandenburg.

Fig. 1341.

Beyrichia Bohemica, Barr. Ordovician; Vinice, Bohemia.

Tetradella, Ulrich. Valves marked by four more or less curved vertical ridges which are ventrally united; one or both of the inner ridges sometimes duplex, or all four may be split up into separate nodes. Ordovician and Silurian.

Ceratopsis, Ulrich. Distinguished from the last by the remarkable process which arises from the extremity of posterior ridge. This may be straight and horn-like with one of the edges toothed, or expanded. Ordovician.

Bollia, Jones and Holl. Valves with a central looped or horseshoe-shaped ridge, the free upper extremities of which are often bulbous. Ordovician to Carboniferous.

Drepanella, Ulrich. Valves depressed convex, sub-oblong, with a more or less complete, often sickle-shaped, sharply elevated marginal ridge, within which the surface exhibits two or more usually distinct nodes. Ordovician.

Family 3. **Cytheridae.** Zenker.

Minute shells of generally elongate-oval, reniform, or sub-quadrate outline, and of dense structure. Surface smooth, punctate, nodulose, striate or spinose; hinge generally denticulated, the right valve with two teeth in most cases, and the left with corresponding pits.

Cythere, Müller (Figs. 1342, 1343). Shell reniform or sub-quadrate, usually widest in front; surface ornamented with punctae, nodes, spines, and ridges; hinge teeth strong, placed one at each end of a horizontal bar which fits into a corresponding furrow and sockets of the left valve. In the sub-genus *Cythereis*, Jones (Fig. 1344), the connecting bar of the hinge is wanting. Cretaceous to Recent.

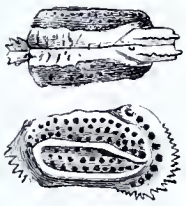


Fig. 1342.

Cythere Edwardsi, Roem. sp. Miocene; Léognan, near Bordeaux. $^{22}/_{1}$ (after Bosquet).

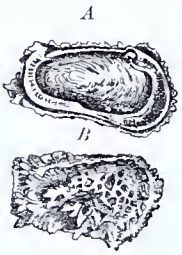


Fig. 1343.

Cythere Dunemelensis, Norman. Pleistocene; Jordan Hill, England. *A*, Interior of left valve. *B*, Exterior of right valve, enlarged (after Brady).

Cytheridea, Bosq. (Fig. 1345). Differs from *Cythere* in having hinge beset with row of small teeth in right valve, often interrupted in the middle, and with corresponding pits in the left. Jura to Recent.

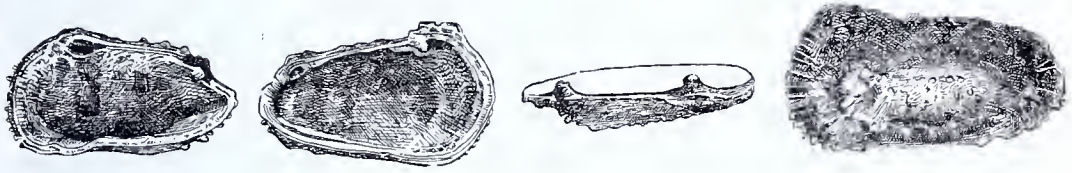


Fig. 1344.

Cythereis quadrilatera, Roemer. Gault; Folkestone. $^{25}/_{1}$ (after T. Rupert Jones).

Fig. 1345.

Cytheridea Muelleri, Münst. sp. Eocene; Colwell Bay, England. $^{22}/_{1}$ (after Jones).

Cytherideis, Jones. Shell more or less triangular. Surface smooth, pitted or tuberculate; hinge simple. Cretaceous to Recent.

Family 4. **Thlipsuridae**. Jones.

Minute, reniform, or ovate inequivalve shells, the margin of one valve overlapping that of the other more or less completely; dorsal margin arcuate, ventral sometimes straight or slightly sinuate. Surface with two or more definite pits.

Thlipsura, Jones and Holl. Each valve generally with three pits, one posterior and two in the anterior half. No ornament. Silurian.

Octonaria, Jones. Differs from the last in having the surface of valves raised into a thin spiral or annular ridge which in more typical forms is 8-shaped. Silurian and Devonian.

Phreatura, Jones and K. Distinguished from *Thlipsura* by the strong compression of posterior end of shell, which is further marked by a shallow semicircular pit; a similar but smaller pit present at anterior extremity. Carboniferous.

Family 5. **Cypridae**. Zenker.

Minute, mostly reniform or elongate-ovate, corneous or corneo-calcareous shells, with thin, somewhat unequal valves, one overlapping the other either ventrally or dorsally or both.

Recent *Cypridae* are chiefly fresh-water inhabitants, but this is true in a lesser degree of the fossil forms. All the Palaeozoic representatives are marine, excepting

perhaps certain Carboniferous species. Fossil remains are extraordinarily profuse in certain deposits, and the family is an important rock-builder.

Palaeocypris, Brongt. Shell 0·5 mm. long, sub-ovate, smaller posteriorly than in front; surface granulose and finely hirsute in dorsal region. Carboniferous.

Cypris, Müller (Fig. 1346). Shell reniform or oval, thin, translucent, smooth or hirsute, often punctate; hinge edentulous, somewhat thickened; ventral margin often sinuate. Tertiary to Recent.

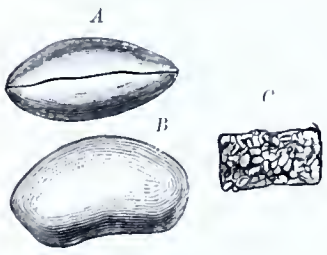


Fig. 1346.

Cypris faba, Desm. Miocene; Oeningen, Switzerland. *A*, Side, and *B*, Dorsal view. $^{15}/_{1}$ (after Bosquet). *C*, Valves composing fresh-water limestone at Nördlingen.

Cypridea, Bosq. (Fig. 1347). Like *Cypris*, but with small hook-like projection at the antero-ventral angle. Purbeck and Wealden.

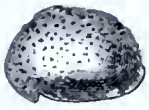


Fig. 1347.

Cypridea Waldensis, Sowb. Wealden; Oberkirchen, Hanover. $^{15}/_{1}$.

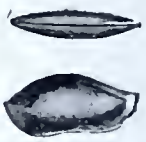


Fig. 1348.

Bairdia curta, M'Coy. Carboniferous Limestone; Ireland. $^{15}/_{1}$ (after Kirkby).

Bairdia, M'Coy (Fig. 1348). Shell sub-triangular or rhomboidal, with the greatest height near the middle, generally smooth, both extremities narrowly rounded or pointed. Dorsal margin more or less strongly convex; hinge formed by overlapping edge of left valve. Ordovician to Recent; maximum in Carboniferous.

Bythocypris, Brady. Shell smooth, reniform, ovate or elliptical; left valve overlapping the smaller right valve usually on both dorsal and ventral margins. Typically Recent, but a number of Palaeozoic forms have also been assigned to this genus.

Macrocypris, Brady. Similar to the last, but generally more elongate, posteriorly more acuminate, and right valve larger than the left. Ordovician and Silurian; Jurassic to Recent.

Pontocypris, Sars. Like *Bythocypris*, except that shell is very delicate, and hinge simple without overlap. Silurian, Carboniferous, Pleistocene, and Recent.

Family 6. **Cytherellidae.** Sars.

Family characters chiefly zoological. Shell minute, inequivalve, thick, calcareous, not notched anteriorly.

Cytherella, Jones (Fig. 1349). Shell oblong or sub-ovate, compressed in front; surface generally smooth, but sometimes undulating and marked with pits and granules. Contact margin of the larger right valve grooved for reception of flange-like edge of smaller left valve. Ordovician to Recent.

Cytherellina, Jones and Holl. Silurian. ? *Pachydomella*, Ulrich. Devonian. *Bosquetia*, Brady. Recent.

Fig. 1349.

Cytherella compressa, Münst. sp. Oligocene; Rüppelmonde, Belgium. $^{22}/_{1}$ (after Bosquet).

Family 7. **Entomidae.**

Shells relatively short, strongly convex, reniform, ovate or rounded quadrate, sub-equivalve, with a more or less well-marked depression near the middle of dorsal region. Surface sculpture concentric or radiate.

Entomis, Jones (Figs. 1350, 1351). Shell sub-ovate or fabiform; valves with a slightly curved sub-median vertical furrow extending to hinge line; in front of furrow occasionally a rounded tubercle. Surface marked generally with raised, concentric,

transverse or longitudinal lines. Ordovician to Carboniferous; very profuse in Devonian.

Entomidella, Jones. Like *Entomis*, but with furrow extending entirely across the valves to ventral edge. Cambrian to Silurian.

Elpe, Barr. Shell reniform, 3 mm. to 7 mm. long, with depression just behind the middle of dorsal slope; posterior half sometimes strongly inflated. Delicate radial ornament. Ordovician and Silurian.

Fig. 1350.

Entomis pelagica, Barr. Lower Devonian (F); Konieprus, Bohemia.

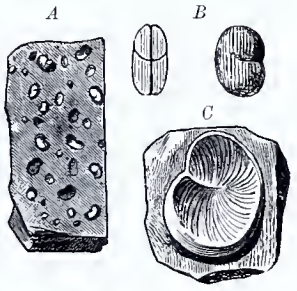


Fig. 1351.

Entomis serrato-striata, Sandb. sp. Upper Devonian; Weilburg, Nassau. *A*, Fragment of matrix, 1/1. *B*, Ventral and lateral aspects, 5/1. *C*, Impression of valve, 9/1.

Family 8. **Cypridinidae.** Sars.

Shells equivalve, sub-elliptical to oblong, convex, smooth or punctate, and sometimes ribbed, especially in posterior half. Anterior end with a notch and hook-like hood overhanging an opening left between edges of valves for protrusion of the lower antennae; posterior extremity frequently acuminate.

Cypridina, Milne-Edw. (Fig. 1352). Shell generally acuminate, oviform, rarely oblong; antero-dorsal edge projecting beak-like over the strongly defined notch; muscle spot large, sub-central, often visible on exterior. Ordovician to Recent.

Cypridinella, J. K. and B. Like *Cypridina*, but having the antero-ventral region projecting somewhat prow-like and generally beyond the hook. Carboniferous.

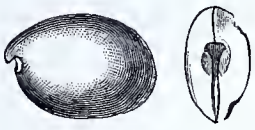


Fig. 1352.

Cypridina primaeva, de Kon. sp. Coal Measures; Braidwood, England. 4/1 (after J. K. and B.).

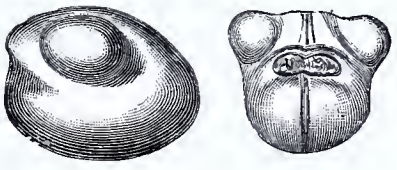


Fig. 1353.

Cypridella Wrightii, J. K. B. Carboniferous Limestone; Cork, Ireland. 8/1 (after J. K. and B.).

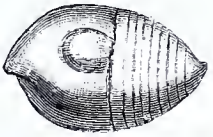


Fig. 1354.

Cyprella chrysalidea, de Kon. Carboniferous Limestone; Cork, Ireland. 4/1 (after J. K. and B.).

Cypridellina, J. K. and B. Differs from the last in having a tubercle or lump above the centre of the valve. Carboniferous.

Cypridella, de Kon. (Fig. 1353). Like *Cypridellina* except that it has a curved sulcus behind the tubercle. Carboniferous.

Cyprella, de Kon. (Fig. 1354). Shell much as in the last, but annulate. Carboniferous.

Sulcuna, *Rhombina*, J. K. and B.; *Cyprosis*, *Cyprosina*, Jones. Palaeozoic.

Family 9. **Entomoconchidae.**

Shell sub-globose, more or less inequivalve; front edge truncate and with central portion of margin inturned so as to leave a simple or sinuate slit. Beak not developed.

Entomoconchus, M'Coy; *Offa*, Jones, Kirkby and Brady. Carboniferous.

Geological Range of the Ostracoda.

Undoubted *Ostracoda* are first met with in the Upper Cambrian, and certain problematical remains indicate that they were initiated even earlier. Their post-

Cambrian evolution was very rapid, and during the Ordovician they flourished as greatly as at any subsequent period. The prevailing Ordovician and Silurian types belong to the *Leperditiidae* and *Beyrichiidae*, although toward the close of the Silurian numerous *Cypridae* make their appearance.

Devonian *Ostracoda* are less numerous, but manifest essentially the same types as in the earlier periods. Here, however, the larger *Leperditiidae* are entirely wanting. Although many small species of archaic genera persist in the Carboniferous, the aspect of the fauna is changed by the strong development of *Cyprinidae*. Thereafter but a meagre representation of Ostracods is met with until the Cretaceous, when certain genera, especially *Cythere*, develop a surprising variety and wealth of species. Little difference can be detected between Tertiary Ostracods and their modern descendants.

[The above generic diagnoses of *Ostracoda* have been abridged from a more extended discussion of the group, prepared for this work by Mr. E. O. Ulrich, of Newport, Kentucky.—TRANS.]

Super-Order 4. CIRRIPEDIA. Barnacles. Latreille.[1]

Sessile, mostly hermaphroditic animals, enclosed in a membranous mantle which is often covered with calcareous plates. Body attached by the anterior extremity of the head; obscurely, and at times not at all segmented; posterior portion with at most six pairs of divided legs or cirri, which, however, may be fewer in number or altogether absent.

The typical and best known Cirripedes (*Balanidae* and *Lepadidae*) differ so widely from all other *Crustacea* in their external form, solid calcareous shells, slightly developed respiratory and sensory organs, and especially in their hermaphroditic sexual apparatus, that until 1830 they were commonly classed with the *Mollusca*. About this time J. V. Thompson and Burmeister showed

[1] Literature: A. Recent Forms.

Thompson, J. V., Zoological Researches and Illustrations. I. Cork, 1830.—Discovery of the Metamorphosis in the Lepades, etc. (Phil. Trans. Roy. Soc., Pt. 2), 1835.—*Burmeister, H.*, Beiträge zur Naturgeschichte der Rankenfüssler. Berlin, 1834.—*Martin-Saint-Ange, G. J.*, Mémoire sur l'organisation des Cirripèdes (Mém. Savans. Étrang. Acad. Sci. Paris, VI.), 1835.—*Darwin, C.*, A Monograph of the Sub-Class Cirripedia (Ray Soc., I., II.), 1851-54.—*Hoek, P. P. C.*, Report on the Cirripedia (Rept. Challenger Exped., Zool., VIII., X.), 1883-84.—*Aurivillius, C. W. S.*, Studien über Cirripeden (K. Svensk. Vetensk. Akad. Handl., XXVI., No. 7), 1893.—*Groom, T. T.*, On the Early Development of the Cirripedia (Phil. Trans. Roy. Soc., 185), 1894.—*Hansen, H. J.*, Phyllopoda and Cirripedia. Plankton Expedition, 1895.

B. Fossil-Forms.

Sowerby, J., and *J. de C.*, The Mineral Conchology of Great Britain. London, 1812-30.—*Roemer, F. A.*, Die Versteinerungen des norddeutschen Kreidegebirges. Hanover, 1840-41.—*Darwin, C.*, A Monograph of the Fossil Lepadidae of Great Britain (Palaeont. Soc.), 1851.—A Monograph of the Fossil Balanidae and Verrucidae of Great Britain (*ibid.*), 1854.—*Bosquet, J.*, Monographie des Crustacés fossiles du terrain crétacé du Duché de Limbourg (Mém. Commiss. Carte geol. Néderlande), 1854.—Notice sur quelques Cirripèdes recemment découverts dans les terrains crétacé du Duché de Limbourg. Haarlem, 1857.—*Reuss, A. E.*, Ueber fossile Lepadiden (Sitzungsber. Akad. Wiss. Wien., XLIX.), 1864.—*Woodward, H.*, On Turrilepas, etc. (Quar. Journ. Geol. Soc., XXI.), 1865.—*Barrande, J.*, Système Silurien du centre de la Bohême., I. Suppl. 1872.—*Seguenza, G.*, Ricerche palaeontologiche intorno di Cirripedi terziarii della Provincia di Messina, Pts. I., II. Naples, 1873-76. *Marsson, J.*, Die Cirripeden und Ostracoden der weissen Schreibkreide der Insel Rügen (Mittheil. naturw. Ver. Neu-Vorpommern und Rügen, XII.), 1880.—*Zittel, K. A.*, Bemerknugen über einige fossilen Lepaditen aus dem lithographischen Schiefer und der oberen Kreide (Sitzungsber. Bayer. Akad. Wiss., XIV.), 1884.—*Faber, C. L.*, Remarks on some Fossils of the Cincinnati Group (Journ. Cincin. Soc. Nat. Sci., IX.), 1887.—*Hall, J.*, and *Clarke, J. M.*, Palaeontology of New York, VII. p. 209, 1888.—*Clarke, J. M.*, Notes on certain Fossil Barnacles (Amer. Geol., XVII.), 1896.—*Matthew, G. F.*, On occurrence of Cirripeds in the Cambrian (Trans. N. Y. Acad. Sci., XV.), 1896.—*Logan, W. N.*, Cirripeds from Cretaceous of Kansas (Kansas Univ. Quar., VI.), 1897.

that these Cirripedes pass through a nauplius stage, and that directly before attachment both *Balanus* and *Lepas* undergo a *Cypris*-stage, thus showing very clearly their relation to the *Eucrustacea*.

All Cirripedes are marine animals. Those with calcareous shells attach themselves to stones, wood, mollusks, crabs, corals, and sea plants, and often cover rocky coasts in myriad numbers. Some genera (*Coronula*, *Chenolobia*) embed themselves in the thick skin of whales and dolphins; some (*Pyrgoma*, *Palaeocreusia*) bore into corals or shells of mollusks, and others lead a parasitic existence in the abdominal cavity of Decapods or within the shells of other Cirripedes. Most barnacles inhabit shallow water, but certain genera occur at great depths, from 1900 to 2000 fathoms (*Scalpellum*, *Verruca*). Many of the living families are naked, and naturally only those possessing shells (*Thoracica*) have left fossil remains, although some of the tubular cavities in molluscan shells may have been perforated by naked Cirripedes. Fossil forms occur sparingly in the older strata, and do not become abundant until near the close of the Tertiary.

Order 1. THORACICA. Darwin.

Body indistinctly segmented, and enclosed in a membranous mantle in which calcareous plates are usually developed. Mostly hermaphroditic, sometimes with complemental males.

Family 1. **Lepidocoleidae.** Clarke.

Body covered with two vertical columns of overlapping plates, those of one series alternating with those of the other. Terminal or caudal plate axial. Basal or cephalic portion of the body with a ventral curvature. Apices of the plates on the dorsal margin. No accessory plates.

Lepidocoleus, Faber (Fig. 1355). Elongate, blade-shaped; dorsal edge the thicker, ventral edge sharper and linear. The two series of plates make a complete enclosure, being interlocked on the dorsal edge, but are only in apposition on the ventral edge, where they were undoubtedly capable of dehiscence for the protrusion of the appendages. Most primitive genus of the group. Ordovician to Devonian.

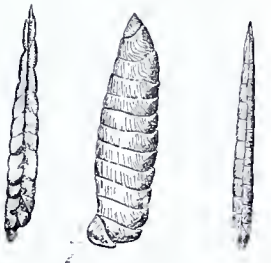


Fig. 1355.

Lepidocoleus Sarlei, Clarke. Silurian; Rochester, New York. Dorsal, lateral, and ventral views.

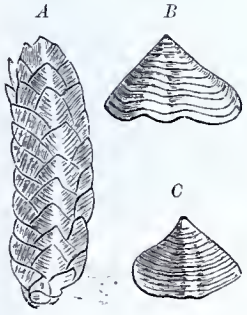


Fig. 1356.

Turrilepas Wrightianus, de Koninck. Silurian; Dudley, England. *A*, Complete individual, 1/1. *B*, *C*, Isolated plates, enlarged (after Woodward).

Family 2. **Turrilepadidae.** Clarke.

Body with four to six vertical columns of triangular plates, two of the columns being small, accessory, and sometimes much modified in shape. Caudal plate patelliform, axial.

Turrilepas, Woodw. (*Plumulites*, Barr.), (Fig. 1356). Body elongate-conical with four to six columns of large triangular overlapping scales, some of which are keeled in the middle. Besides having concentric striae, surface may be radially lined or punctated. Cambrian (?) to Upper Devonian.

Strobilepis, Clarke. Composed of four columns of overlapping plates, two of which are of large and equal size. Of the other two intervening columns, one consists of a few very small plates, and the other is modified into a series of grooved spines which

appear to overlap one another at their bases, and to lie opposite the column of small plates. Caudal extremity terminated by a circular, conical, axial plate, against the sides of which lies the first plate in each column. Middle Devonian.

Family 3. **Lepadidae.** Darwin. (Goose Barnacles.)

Shell pedunculated, composed mainly of the paired terga and scuta, the unpaired carina, and a variable number of small calcareous plates, some of which cover the flexible pedunele; others take part in the capitulum. The calcareous plates are never fused.

Archaeolepas, Zittel (Fig. 1357). Peduncle flattened, the two principal surfaces with four to six, the narrow sides with two columns of small scales. The capitulum is composed of triangular scuta, two large trapezoidal terga, a short unpaired carina, and a minute rostrum. Upper Jura.

Fig. 1357.

Archaeolepas Redtenbacheri, Opp. sp. Lithographic Slates; Kelheim, Bavaria. 1/1. *C*, Carina; *R*, Rostrum; *S*, Scutum; *T*, Tergum.

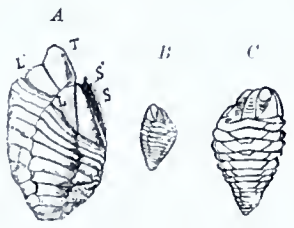


Fig. 1358.

A, Loricula laevissima, Zitt. Senonian; Dülmen, Westphalia. 1/1. *B, C, L. Syriaca*, Dames. Cenomanian; Lebanon. 1/1 and 2/1.

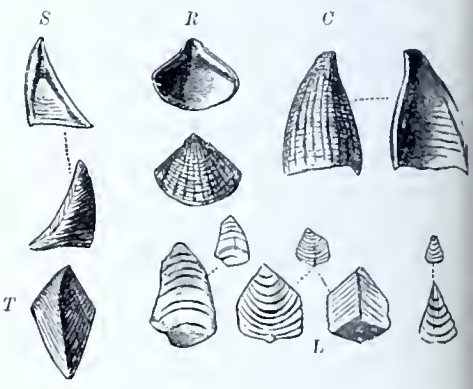


Fig. 1359.

Pollicipes laevissimus, Quenst. Upper Cretaceous; Lüneburg, Belgium. *C*, Carina; *L*, Lateralia; *R*, Rostrum (?); *S*, Scutum. 1/1.

Loricula, Sowb. (Fig. 1358). Peduncle squamous. Capitulum with two scuta, two terga, four lateralia, and a very narrow carina. Cretaceous.

Pollicipes, Leach (*Polylepas*, Blainv.), (Fig. 1359). Capitulum composed of numerous (eighteen to one hundred) plates, among which the scuta, terga, rostrum, and carina are distinguishable by their size. Lateralia generally in two columns. Peduncle membranous with minute scales. Upper Jura to Recent.

Fig. 1360.

Scalpellum Gallicum, Hébert. Upper Cretaceous; Meudon, near Paris. 2/1 (after Hébert).

Squama, Stramentum, Logan. Upper Cretaceous (Niobrara); Kansas.

Scalpellum, Leach (Figs. 1360-1362). Capitulum with twelve to fifteen pieces. Terga and scuta much larger than in *Pollicipes* and of very characteristic form. Carina narrow, long, with arched surface. Peduncle covered with fine scales, rarely naked. Cretaceous to Recent.

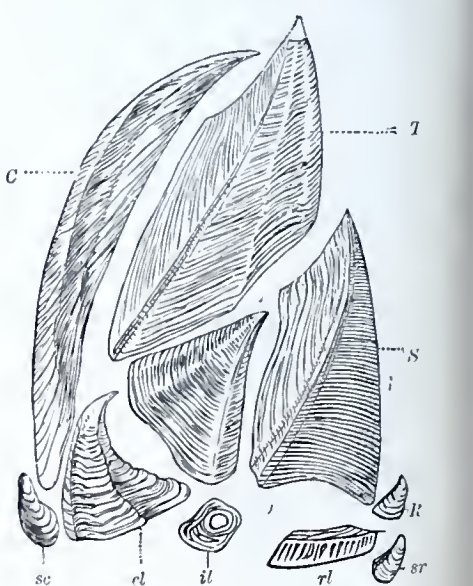


Fig. 1361.

Capitulum of *Scalpellum fossulum*, Darwin. Upper Cretaceous; Norwich, England. 2/1. *C*, Carina; *L*, Laterale superius (upper latus); *R*, Rostrum; *S*, Scutum; *T*, Tergum; *cl*, Carino-latus; *il*, Infra-median latus; *rl*, Rostral latus; *sc*, Sub-carina; *sr*, Sub-rostrum (after Darwin).

Lepas, Linn. (Fig. 1363). Peduncle naked. Capitulum consisting of only two very large triangular scuta, two small terga, and a single carina. Pliocene and Recent.

Poecilasma, Darwin. Capitulum consisting of three, five, or seven pieces. Carina extending only to base of the terga, the latter sometimes wanting. Scuta sub-oval. Tertiary and Recent.

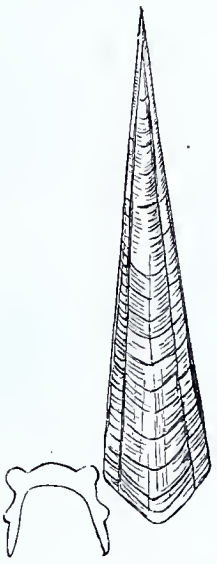


Fig. 1362.

Scalpellum fossulum, Darwin. Carina much enlarged (after Darwin).

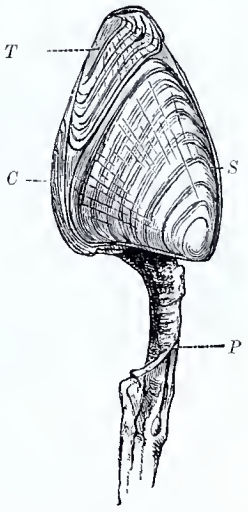


Fig. 1363.

Lepas anatifera, Linn. Recent; Mediterranean *C*, Carina; *P*, Peduncle; *S*, Scutum; *T*, Tergum.

Family 4. **Verrucidae.** Darwin.

Shells sessile and composed of six pieces. Of the scuta and terga only one is free, the other plate in each being fused with the rostrum or carina.

The solitary genus *Verruca*, Schum., ranges from the Cretaceous to Recent.

Family 5. **Balanidae.** Darwin. (Acorn Barnacles.)

Shell obtusely conical, circular, or oval in cross section, with broad calcareous cellular base; composed of four to ten lateralia, more or less completely fused at their sides, and two pairs of free terga and scuta which close the upper aperture like an operculum.

Of the lateral plates which compose the crown-shaped immovable test, two are designated as *carina* and *rostrum*, the pieces lying between and occurring in pairs being called *lateralia*. If additional plates are inserted among the lateralia, they are termed according to their position *rostro-* or *carino-lateralia*. The *scuta* and *terga* lie free on the back of the animal, and in fossil forms are generally lost. They have a very characteristic form, and hence are of great systematic importance. Since among fossil species, however, only the marginal plates are for the most part preserved, the determination of their structural characters is often quite uncertain.

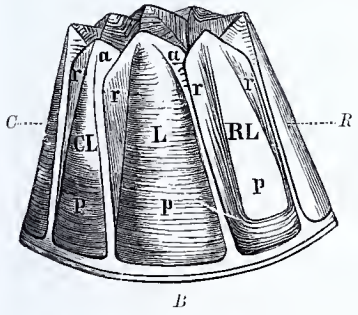


Fig. 1364.

Diagram of the shell of *Balanus*. *B*, Basis; *C*, Carina; *CL*, Carino-lateral compartment; *L*, Lateral compartment; *R*, Rostrum; *RL*, Rostro-lateral compartment. Each valve or "compartment" consists of a central "paries" (*p*) flanked by "alae" (*a*) or "radii" (*r*).

Fig. 1365.

Scutum and tergum of *Balanus*. *A*, External aspect of tergum, showing "spur" below and "beak" above. *B*, Internal view of scutum, showing muscular scar (*x*). *C*, Internal view of tergum (after Darwin).

Balanus, Lister (Figs. 1364-1367). Shell low, conical or cylindrical, composed of

six pieces. Opercular plates sub-triangular; base membranous or calcareous. Eocene to Recent.

Protobalanus, Whitf. Composed of twelve plates, of which the carina is the largest; rostrum small, lateralia in five pairs, fused only near the base. Middle Devonian.

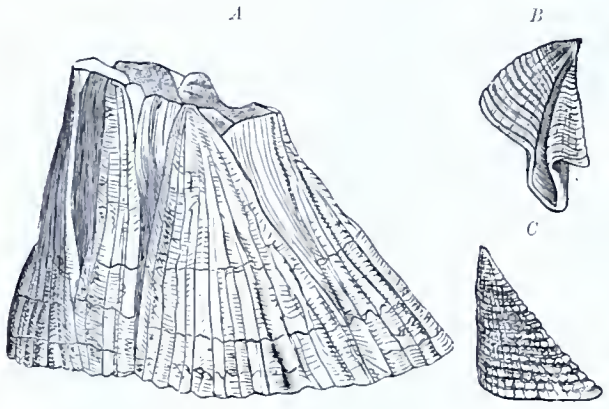


Fig. 1366.

Balanus concavus, Bronn. Crag; Sutton, England. *A*, Shell. *B* Tergum. *C*, Scutum. 1/1 (after Darwin).

Acasta, Leach. Shell composed of six solid pieces. Base calcareous, cup-shaped; attached to sponges and Alcyonarians. Pliocene and Recent.

Pyrgoma, Leach (*Creusia*, Blainv.). Shell formed of a single piece. Base cup-shaped or sub-cylindrical; attached to corals. Lower Devonian. Tertiary and Recent.

Palaeocreusia, Clarke (Fig. 1368). Shell in one piece, with a deep cylindrical base; attached to corals. Lower Devonian.

Coronula, Lam. Composed of six lateralia, with thin, deeply folded walls dividing

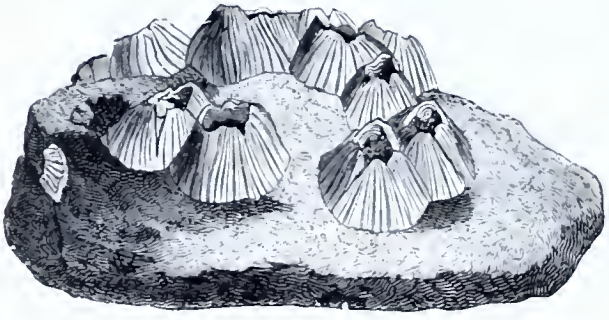


Fig. 1367.

Balanus pictus, Munst. Miocene; Dischingen, Württemberg.

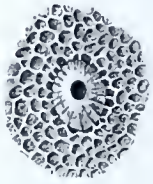


Fig. 1368.

Palaeocreusia devonica, Clarke. Embedded in *Farosites*. Corniferous; Le Roy, New York.

the interior space into chambers which open at the lower side of the shell. Base membranous; parasitic on whales. Pliocene to Recent.

Chthamalus, Ranz (*Euraphia*, Conrad). Shell depressed, composed of six pieces. Base membranous. Cretaceous, Miocene, and Recent.

Pachylasma, Darwin. Shell in the young with eight pieces, which afterwards become six, or by coalescence of the lateralia are apparently reduced to four. Base calcareous. Pliocene to Recent.

Super-Order 5. MALACOSTRACA. Latreille.

Eucrustacea having, in recent forms, a constant number (twenty or twenty-one) of segments. Cephalothorax composed of thirteen segments, and bearing the same number of appendages. Abdomen distinct, heptamerous (except in the Phyllocarida), the terminal joint being known as the telson.

Under this head are included the orders *Phyllocarida*, *Stomatopoda*, *Decapoda*, and *Arthrostraca*, all of which have fossil representatives.

Order 1. PHYLLOCARIDA. Packard. (*Leptostraca*, Claus.)[1]

Body composed of five cephalic, eight thoracic, and two to eight abdominal segments. Head and thorax covered by a thin chitinous or partially calcified carapace, which may be in a single piece or divided into separate valves by a straight, unarticulated, single or double hinge. In front of the carapace is a narrow movable plate or rostrum. The head bears two pairs of antennae, and stalked compound eyes. Thoracic segments with soft phyllopodiform legs. Abdomen composed of annular segments, and often ends in a spiniform caudal plate (telson) provided with lateral spines.

The recent genus *Nebalia* (Fig. 1370) is regarded by Packard and Claus as the surviving representative of ancient Crustacean types, very numerous during the Palaeozoic, which had been previously classed with the *Phyllopoda*, but more properly form a distinct group (*Phyllocarida*) connecting the *Entomostraca* with the *Malacostraca*. The genus is very generalised, combining Copepod, Phyllopod, and Decapod-like features with other more fundamental characters of its own. Upon it is based largely the definition of the order, but some of the extinct families show structural differences from the living type which will eventually require their removal from this association.

Cephalic appendages have not been satisfactorily determined in any fossil species, although traces of them have been noticed in a few genera (*Cryptozoe*, *Ceratiocaris*, *Rhinocaris*). In the absence of contrary evidence there is every reason to suppose that the appendages of the head, thorax, and abdomen were on the type of *Nebalia*, since there is such close correspondence in the form of carapace, rostrum, and abdomen. Owing to the non-preservation of limbs, distinctions within the group are based principally on variations in the structure of the carapace, and in the number of body segments. Several fossil genera (*Echinocaris*, *Rhinocaris*, *Mesothyra*) bear a distinct optic node or pit, suggesting a sessile simple eye in contradistinction to the stalked faceted eye of *Nebalia*. In these genera, also, large cuspidate masticatory organs have been found, which were apparently attached only by means of muscles;

[1] Literature:

Salter, J. W., On some new Fossil Crustacea, etc. (Quar. Journ. Geol. Soc., XII. p. 26, XIX. p. 75), 1856-62.—On New Silurian Crustacea (Ann. Mag. Nat. Hist., V. p. 153), 1860.—*Hall, J.*, Palaeontology of New York, III., 1859.—16th Ann. Rept. N.Y. State Cabinet Nat. Hist. 1863. —*Woodward, H.*, On a new Genus of Phyllopodous Crustacea (Quar. Journ. Geol. Soc., XXII. p. 503), 1866.—Geol. Mag., IX. pp. 433, 563, 1872; IX. pp. 386, 444, 1882; II. pp. 345, 385, 460, 1885.—*Claus, C.*, Ueber den Bau und die systematische Stellung von Nebalia (Zeitschr. wissensch. Zool., XXII.), 1872.—*Barrande, J.*, Système Silurien du centre de la Bohême, I. Suppl. 1872.—*Whitfield, R. P.*, Notice of new Forms of Fossil Crustacea, etc. (Amer. Journ. Sci. [3], XIX.), 1880.—*Clarke, J. M.*, New Phyllopod Crustacea from the Devonian (Amer. Journ. Sci. [3], XXIII.), 1882.—New Discoveries in Devonian Crustacea (*ibid.* XXV.), 1883.—Ueber deutsche oberdevonische Crustaceen (Neues Jahrb., I. p. 178), 1884.—On the Structure of the Carapace in Rhinocaris, etc. (Amer. Nat., XXVII. p. 793), 1893.—14th Rept. State Geol. N.Y. I., 1898.—*Packard, A. S.*, A Monograph of the Phyllopod Crustacea of North America (12th Ann. Rept. U.S. Geogr. Geol. Surv. Terr.), 1883.—*Beecher, C. E.*, Ceratiocaridae from the Upper Devonian Measures (2nd Geol. Surv. Penn. Rept. PPP), 1884.—*Jones, T. R.*, and *Woodward, H.*, Various Papers in Geol. Mag., I.-X., 1884-94, and Reports 1-12 of Comm. on Fossil Phyllopoda Brit. Assoc. Adv. Sci., 1883-95.—*Novák, O.*, Remarques sur le genre Aristozoe (Sitzungsber. böhm. Akad. Wissensch. p. 239) 1885.—(*Ibid.* p. 674), 1886.—On Occurrence of a New Form of Discinocaris in Bohemia (Geol. Mag. [3], IX. p. 148), 1892.—*Sars, G. O.*, Report on the Phyllocarida (Leptostraca) Rept. Challenger Expedition, XIX., 1887.—*Hall, J.* and *Clarke, J. M.*, Palaeontology of New York, VII., 1888.—*Whitfield, R. P.*, New Genus of Phyllocaridae (Bull. Amer. Mus. Nat. Hist., VIII.), 1896.—*Jones, T. R.*, and *Woodward, H.*, Monograph of the British Palaeozoic Phyllopoda (Phyllocarida, Packard), Part III. (Palaeontogr. Soc.), 1898.

these are compared by Woodward with the gastric teeth of the lobster (Fig. 1369).

Sub-Order A. NEBALIINA. Clarke.

Carapace folded, univalved, and rostrate.

Family 1. Nebaliidae. Baird.

Cephalic appendages five, thoracic eight, abdominal eight, terminating in two caudal spines. No metamorphosis; development direct.

Fig. 1369.

Gastric teeth of *Echinocaris punctata*, Hall. Hamilton; Pratt's Falls, New York. 1/1.

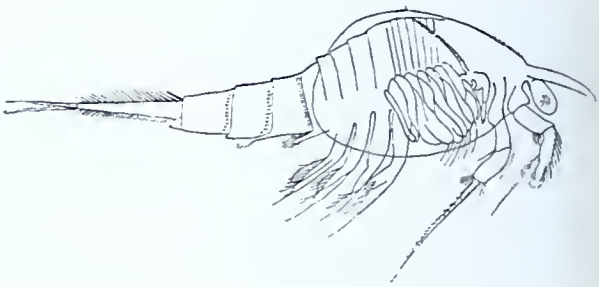


Fig. 1370.

Nebalia Geoffroyi, M. Edw. Recent; Mediterranean. 8/1.

Nebalia, Leach (Fig. 1370). Represented by a few species inhabiting shallow waters of northern seas. *Paranebalia* and *Nebaliopsis* are also Recent and marine.

Sub-Order B. HYMENOCARINA. Clarke.

Nebalia-like forms with folded univalved carapace; rostrum wanting (?).

Family 1. Hymenocaridae. Salter.

Body with eight to nine thoracic and abdominal segments, and six caudal spines in three pairs.

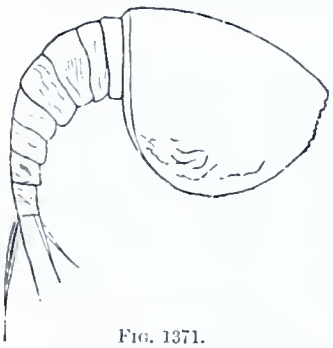


Fig. 1371.

Hymenocaris vermicauda, Salter. Upper Cambrian; Dolgelly, Wales. (after Salter). 1/1.

Hymenocaris, Salter (Fig. 1371). Carapace narrow in front, very broad posteriorly, convex; surface smooth or faintly lined. Cambrian; Wales.

[*Ribeiria*, Sharpe. Arched, univalved bodies with strong beaks, muscular scars and sub-cardinal ridge. These fossils have been referred to the *Phyllocarida*, *Pelecypoda*, and *Gastropoda*. There is no satisfactory evidence of their Crustacean nature.]

Sub-Order C. CERATIOCARINA. Clarke.

Carapace bivalved, with a median symphysis and a free rostrum.

Family 1. Ceratiocaridae. Salter.

Carapace pod-shaped, smooth, and without eye-nodes.

Ceratiocaris, M'Coy (*Entomocaris*, Whitf.), (Fig. 1372). Valves of carapace elongate, sub-ovate, or sub-quadrate, narrow in front, sub-truncate, but not incurved behind.

Surface without nodes or carinae. Antennae (?) obscure; supposed gastric teeth large, cuspidate. Rostrum lanceolate. Body segments fourteen or more, four to seven extending beyond the carapace, some of them with obscure branchial appendages (uropods). Telson long, spinose on the edges; two lateral appendages or cercopods. Abundant in Ordovician and Silurian; Europe and North America.

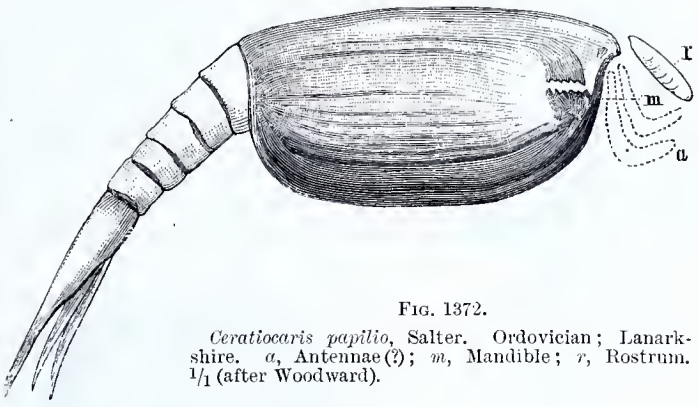


Fig. 1372.

Ceratiocaris papilio, Salter. Ordovician; Lanarkshire. *a*, Antennae (?); *m*, Mandible; *r*, Rostrum. 1/1 (after Woodward).

Cardiolites, Nich. Supposed tracks of *Ceratiocaris* (?). Silurian; Scotland.

Caryocaris, Salter. Carapace smooth, narrow, sub-acute in front, thick. Abdomen unknown; caudal plate with three spines. Cambrian; Wales.

Physocaris, Salter. Carapace bladder-shaped, pointed in front, bivalved (?), smooth. Abdomen smooth; telson longer than the cercopods. Silurian.

Lingulocaris, Salter; *Saccocaris*, Salter. Very imperfect remains of Crustacean bodies. Lingula Flags; Wales.

Acanthocaris, Peach. Carapace small, with a blunt snout in front; surface smooth. Body segments numerous, seven exposed beyond the carapace. Telson long; cercopods short or rudimentary. Lower Carboniferous; Scotland.

Xiphidiocaris, Jones and Woodw. (emend.). Known only by its long curved blade-like telson. Silurian (Ludlow); England. (*X. ensis*, Salter.)

Cryptozoe, Packard. Carapace smooth, broadly rounded in front; imperfectly known. Coal Measures; Illinois. (*C. problematicus*, Packard.) Probably congeneric with the Carboniferous species, *Ceratiocaris Oretonensis*, and *C. truncata*, Woodw., in which traces of four cephalic appendages have been found.

Colpocaris, Meek. Carapace smooth, with deep anterior marginal sinus and sharp extremity. Caudal plate with three spines. Lower Carboniferous; Kentucky.

Strigocaris, Vogdes (*Solenocaris*, Meek). Carapace narrow and elongate, with longitudinally striated surface; very imperfectly known. Lower Carboniferous; Kentucky.

Nothozoe, Barrande, may belong in this association. Ordovician; Bohemia.

Phasganocaris, Novák. Known only from the abdomen and telson. Last segment long, cylindrical, with strong articulation. Telson articulated to the cercopods by deep sockets; edges spinose. Surface scaly. Lower Devonian; Bohemia.

Macrocaris, Miller. Carapace valves very narrow in front, broad behind, strongly lineate. Body segments numerous. Lower Carboniferous; Kentucky.

Family 2. **Echinocaridae**. Clarke.

Carapace elongate or oval, with nodes (muscular or segmental) in the cephalic region, one of which in each valve may be ocular but bears no optic pit; one or more lateral carinae usually present. A free rostrum has been observed in some genera.

Echinocaris, Whitf. (Figs. 1369, 1373). Hinge short, carapace sub-oval, broad in front, not incurved behind, no postero-lateral spinules; a single sigmoid carina on each valve, sometimes a small accessory ridge near the hinge. Surface punctate and pustulose, no longitudinal striations. Of the body segments, six are exposed and bear small

spines on their surface and posterior margins. Telson and cercopods are spines of unequal size. Middle and Upper Devonian; North America.

Pephricaris, Clarke (Fig. 1374). Carapace as in the last, but without the lateral carinae. Margins provided with a single row of long recurving spines. Three or four abdominal segments protrude beyond the carapace, the last two having a single pair of long spines. Upper Devonian; New York.

Aristozoe, Barr. (*Bactropus*, Barr.). Carapace with cephalic node well developed, but without lateral carinae. But one abdominal segment known, and this is very long, cylindrical, with an intricate hinge at the articulation with the caudal spines. Telson a long spine with a row of spinules on each lateral edge. Novák has shown that of Barrande's three species, *Aristozoe regina*, *Bactropus longipes*, and *Ceratiocaris debilis*, the first represents the carapace, the second the last abdominal segment, and the third the telson of one form, *A. regina*. Devonian: Bohemia. Species referred to the same genus have been described from the Cambrian of North America and Devonian of Germany and Russia.

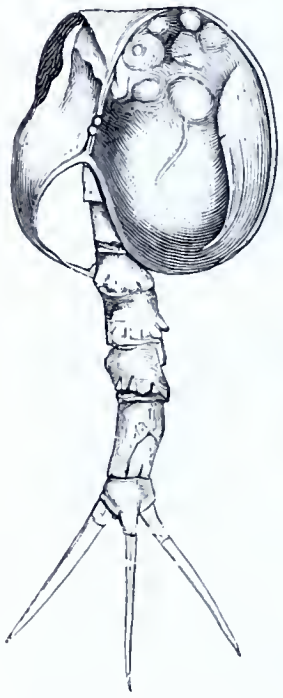


Fig. 1373.

Echinocaris punctata, Hall sp. Hamilton Group; Pratt's Falls, New York. 1/1 (after Beecher).

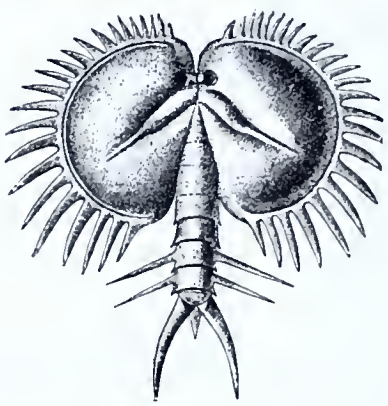


Fig. 1374

Pephricaris horripilata, Clarke. Chemung Group; Alfred, New York. 1/1 (after Clarke).

Orozoe, *Callizoe*, Barrande, are presumably allied to *Aristozoe* (Novák). Silurian; Bohemia. *Zonozoe*, Barr., and *Solenocaris*, Young, are not Crustacean.

Eleutherocaris, Clarke. Carapace elongate-subquadrate, truncate in front, incurved behind; rostrate (?). Broad, obscure nodes in the cephalic region; lateral carinae single, anterior, and very short. Body segments unknown; caudal plate with a slender telson and cercopods of equal length. Surface of all known parts more or less strongly tuberculated. Upper Devonian; New York.

Ptychocaris, Novák. Valves elongate-subquadrate, posterior margin sloping or slightly incurved. Cephalic region with a cluster of small nodes in front, and two larger nodes behind. Lateral region with a single long sigmoid carina. Surface striated with raised longitudinal lines. Abdomen and tail unknown. Lower Devonian; Bohemia.

Elymocaris, Beecher. Surface of carapace evenly convex, smooth, without lateral carina; hinge line long; posterior margin convex; cephalic nodes obscure; rostrum not observed. Abdomen with two exposed segments; caudal plate short, with broad, convex, rapidly tapering telson and two cercopods, setigerous on their inner margins. Middle Devonian; New York. Upper Devonian; Pennsylvania.

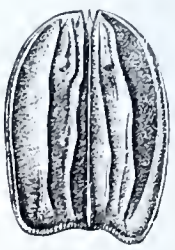


Fig. 1375.

Tropidocaris bicarinata, Beecher. Chemung; Warren, Penn. Carapace and rostrum. 1/1 (after Hall and Clarke).

Tropidocaris, Beecher (Fig. 1375). Carapace with truncate posterior margins; ocular node well defined, other cephalic nodes obscure; rostrum narrow and ridged; surface of valves with several strong longitudinal carinae. Abdomen with two exposed segments, which are sub-cylindrical and without spinules. Upper Devonian and Lower Carboniferous; Pennsylvania.

Emmelezoe, Jones and W. Valves of carapace elongate, narrow, and with distinct ocular node; other cephalic nodes wanting. Surfaces with fine longitudinal raised striae. Abdomen unknown. Silurian.

Sub-Order D. RHINOCARINA. Clarke.

Carapace with a free rostrum and narrow median dorsal plate separated from the valves by a straight or slightly curving hinge at each side. Ocular nodes clearly defined, with a distinct optic pit at the summit.

Family 1. Rhinocaridae. Clarke.

Valves articulated by interlocking at the single point where they come in contact. Abdominal segments two to three. Posterior margin of carapace concave and spined.

Rhinocaris, Clarke (Fig. 1376). Carapace smooth, with fine raised longitudinal striae; divergent, branching furrows radiating backward from the eyes. Lateral carina very faint. Abdomen with two or three free segments, the last much longer than the others; all diagonally striated or chevroned. Caudal plate with a broad telson and two long and slender cercopods fimbriated on their margins. Middle Devonian; New York.

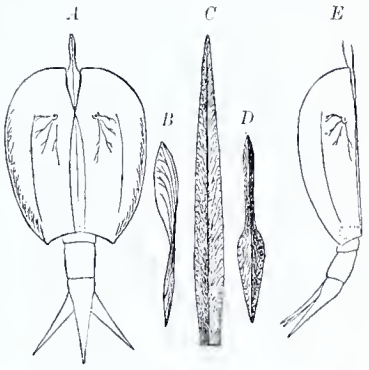


Fig. 1376.

Rhinocaris columbina, Clarke. Hamilton Group; Canandaigua Lake, New York. *A*, *E*, Dorsal and lateral views of animal. *B*, *D*, Same of rostrum, enlarged. *C*, Median plate, enlarged.

Mesothyra, Hall and Clarke (Fig. 1377). Carapace large, valves distinctly interlocking at point of contact. Lateral carinae strong, crenulated at the summit. Abdomen with two broad, exposed segments. Telson shorter than the cereopods, the latter setigerous. Upper Devonian; New York.

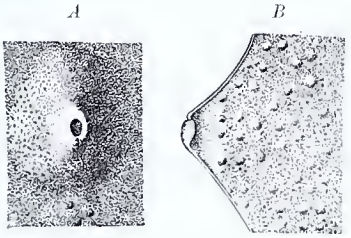


Fig. 1377.

Mesothyra Occani, Hall. Portage Group (Upper Devonian); Ithaca, New York. *A*, Eye. *B*, Hinge of right valve. 1/1.

Dithyrocaris, Scouler (*Argas*, Scouler). Very similar in aspect to *Mesothyra*, with the junction line of the valves overlapped by a (free?) rugose ridge or narrow interstitial plate. Rostrum not observed. Devonian and Carboniferous; Scotland. *Rachura*, Scudder, known only from the abdomen and telson, is probably allied to *Dithyrocaris*. Carboniferous; Illinois.

Chaenocaris, Jones and W. Carapace valves with a very strong lateral ridge and without posterior spine. Carboniferous; Scotland and Belgium.

Sub-Order E. DISCINOCARINA. Clarke.

Sub-circular or oval shields with a triangular rostrum filling an anterior notch Surface ornamented with raised concentric lines. Substance chitinous.

Family 1. **Discinocaridae.** Woodward.

Test convex, sometimes mesially ridged; in a single piece.

Discinocaris, Woodw. Shield sub-circular, rostral notch and rostrum angular. Abdominal segments and caudal spines have been referred to this genus by Jones and Woodward. Silurian; Great Britain, Bohemia.

Fig. 1378.

Dipterocaris vetustus, d'Arch. and Vern. Devonian; Eifel. 1/1.

Aspidocaris, Reuss. Similar to *Discinocaris*. Raibl Beds (Trias); Hallstadt.

Dipterocaris, Clarke (Fig. 1378). Shield with a deep posterior notch, shorter than the anterior or rostral notch. Sides of shield sloping. Silurian; Scotland. Upper Devonian; New York.

Family 2. **Peltocaridae.** Salter.

Shields mesially sutured.

Peltocaris, Salter. Circular shields with a rounded rostral notch and plate. Abdomen unknown. Ordovician; Great Britain.

Aptychopsis, Barr. (Fig. 1379). Like *Peltocaris*, but with the rostral notch angular. Silurian; Bohemia and Great Britain.

Pinnocaris, Etheridge. Similar to *Dipterocaris*, but bivalved. Ordovician; Scotland. (*P. Lapworthi*, Etheridge jun.)

Fig. 1379.

Aptychopsis primus, Barr. Ordovician (D); Branik, Bohemia. 1/1 (after Barrande).

Addendum.

A number of generic names, such as *Cardiocaris* (Fig. 1380), *Ellipsocaris*, *Pholadocaris*, Woodward, and *Spathiocaris*, Clarke, have been applied to Devonian fossils which closely resemble the Silurian *Discinocaris*, of whose Crustacean nature there seems to be no doubt. Some of these bodies, however (*Cardiocaris*), have been found in the living chamber of Goniatites (*G. intumescens*), and have undoubtedly served as opercula or aptychi of these Cephalopods; of others the nature is not fully understood. *Lisgocaris*, Clarke, is not a Crustacean; *Cryptocaris*, Barrande, is probably the operculum of a Hyolithoid; *Myocaris*, Salter, is stated to be a Pelecypod; *Proricaris*, Baily, was founded on parts of *Ceratiocaris; Crescentilla* and *Pterocaris*, Barrande, are doubtfully Crustacean.

Fig. 1380.

Cardiocaris (*Anaptychus?*) *Roemeri*, Woodw. Upper Devonian; Budesheim, Eifel. 1/1.

[The authorship of the foregoing chapters on *Phyllopoda*, *Cirripedia*, and *Phyllocarida*, as well as the succeeding one on the *Accrata* (*Merostomata*), should be accredited to Dr. John M. Clarke, New York State Palaeontologist. A number of additional figures for illustrating these sections have also been prepared by him expressly for this work, or borrowed from his previous writings.—Trans.]

Order 2. SCHIZOPODA. Latreille.[1]

Small, elongated, aquatic Malacostraca with compound eyes borne on movable stalks, and a large delicate carapace covering the thoracic segments more or less completely; with

[1] Literature:

Jordan, H., and *Meyer, H. v.*, Crustaceen der Steinkohlenformation von Saarbrücken (Palaeontogr., IV.), 1856.—*Salter, J. W.*, Higher Crustacea from British Coal Measures (Quar. Journ. Geol. Soc., XVII.), 1861.—*Etheridge, R.*, Occurrence of Anthrapalaemon in Carboniferous of Scotland (*ibid.* XXXIII.), 1877.—*Whitfield, R. P.*, New Crustacea from the Devonian of Ohio (Amer. Journ. Sci. [3], XIX.), 1880. Also in Ann. N.Y. Acad. Sci., V., 1891.—*Peach, B. N.*, New Crustacea from the Carboniferous of Eskdale (Trans. Roy. Soc., Edinburgh, XXX., pp. 73, 512), 1880.—*Brocchi, P.*, Note sur un Crustacé, etc. (Bull. Soc. Geol. France [3], VIII.), 1880.—*Packard, A. S.*, On the

eight pairs of thoracic feet, which are similarly formed, provided with an exopodite, and in one family (Mysidae) bear freely projecting gills.

The Schizopods bear a superficial resemblance to the macrurous *Decapoda*, and were formerly united with that order. Two principal groups are distinguished, the Mysid and Euphausid, which by some authors are elevated into independent orders. A few fossil remains have been, with some colour of probability, assigned to the Schizopods, such as *Pygocephalus*, Huxley, from the English Coal Measures, and *Crangopsis*, Salter (*Palaeocrangon*, Salter non Schauroth; *Archaeocaris*, Meek), from the Lower Carboniferous of Scotland and base of the Waverly in Kentucky. *Pygocephalus* also exhibits many Stomatopod features.

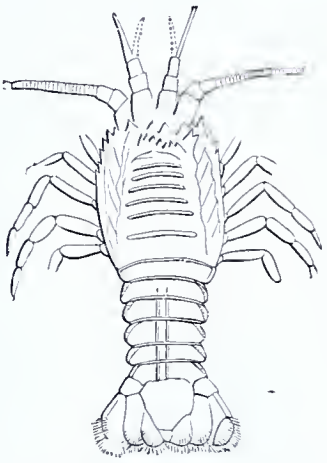


Fig. 1381.

Anthrapalaemon gracilis, M. and W. Coal Measures; Illinois. Restoration, 1/1 (after Meek and Worthen).

Anthrapalaemon, Salter (Fig. 1381), from the Coal Measures of Scotland and Illinois, and *Palaeopalaemon*, Whitfield, from the Devonian of Ohio, are of doubtful position, but more properly classed with the Schizopods than Decapods. The former genus has a curiously subdivided telson, a toothed anterior margin of the carapace, and biramous antennae. *Palaeopemphix*, *Paraprosopon*, and *Oonocarcinus*, Gemmellaro, from the Permo-Carboniferous of Sicily, are for the most part fragmentary remains, but without any decided Decapod features. The same is true of *Pseudogalathea*, Peach, from the Lower Carboniferous of Scotland.

The family *Nectotelsonidae* of Brocchi comprises a few Carboniferous and Permian genera whose relations to the recent *Anaspides* have been suggested by Calman. These are; *Palaeocaris*, Meek and Worthen; *Uronectes*, Bronn (*Gampsonyx*, Jordan), (Fig. 1382); and *Nectotelson*, Brocchi (but not *Acanthotelson*, M. and W.). They show a number of characters common to all *Malacostraca*, but no typical characters of any one order. *Anaspides*, Thomson, living in the mountains of Tasmania, agrees with the extinct genera in the combination of Podophthalmate characters with a completely segmented body and the lack of a carapace; and while having its nearest affinities with the Schizopods, is also closely related to the Amphipods.

Fig. 1382.

Gampsonyx fimbriatus, Jordan. Rothliegendes: Lebach, near Saarbrücken. 1/1.

The proposal to erect a separate order (*Syncarida*, Packard) for this family, including *Anaspides*, seems hardly advisable, although it is plain that many collective characters are here displayed. These peculiar fossil forms indicate that a differentiation of *Thoracostraca* and *Arthrostraca* took place as far back as the Upper Devonian, but distinctive ordinal features are not manifested until much later. [The term *Thoracostraca* (=*Podophthalma*) is used throughout this section to connote the Schizopods, Stomatopods, and Decapods under one head, as distinguished from the sessile-eyed Amphipods and Isopods.]

Order 3. STOMATOPODA. Latreille.[1]

Elongated Malacostraca, in which the compound stalked eyes and first pair of antennae are borne upon distinct movable segments. Carapace small, leaving the last four thoracic segments uncovered. There are five pairs

Syncarida, Gampsonychidae, and Anthracaridae (Mem. Nat. Acad. Sci., III.), 1885. Also in Proc. Boston Soc. Nat. Hist., XXIV., 1889.—*Calman, W. T.*, On the Genus Anaspides, etc. (Trans. Roy. Soc., Edinburgh, XXXVIII.), 1896.—*Ortmann, A. E.*, The Systematic Position of Crangopsis, etc. (Amer. Journ. Sci. [4], IV.), 1897.

[1] Literature:

Münster, G. Graf zu, Beiträge zur Petrefaktenkunde (Heft. III. p. 19; V. p. 76), 1840-42.—*von der Mark, W.*, and *Schlüter, C.*, Neue Fische und Krebse aus der Kreide von Westphalen

of maxillipeds, the second pair being developed into large raptorial limbs, and three pairs of biramous thoracic feet. Abdomen very strongly developed, longer than the anterior part of the body, and its swimming feet bear branchial tufts.

The Stomatopods comprise a single family (*Squillidae*) of nine recent and still fewer fossil genera, with the characteristics of the order. Living forms are inhabitants of tropical and temperate waters of both hemispheres, and prey upon other animals. The oldest fossil form is *Necroscylla Wilsoni*, Woodward, from a concretion in the Coal Measures of Cossall, England. It is founded upon an abdominal fragment 21 mm. long, showing five segments and a well-preserved telson, and bears some resemblance to the abdomen of *Squilla*. *Squilla* itself dates back to the Upper Jura (Lithographic Slates), and species are known from the Cretaceous of Lebanon, Eocene of Monte Bolca, and Highgate, England.

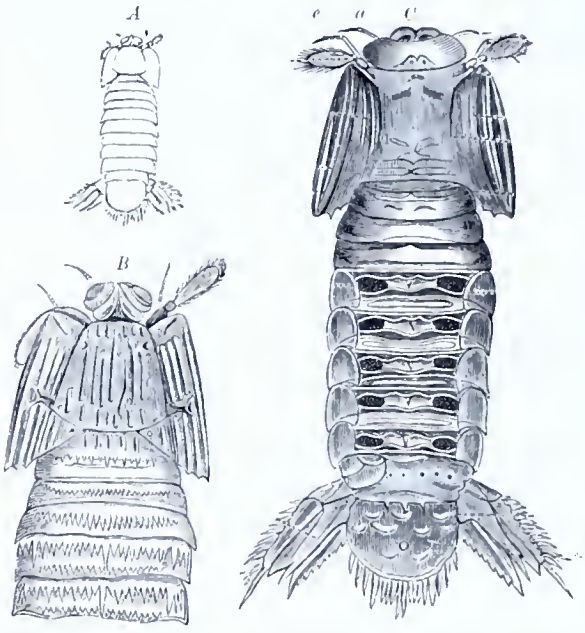


Fig. 1383.

Scalda pennata, Münst. Upper Jura; Bavaria. *A*, *B*, Dorsal views, 1/1 and 3/1. *C*, Ventral aspect, 3/1. *a*, *e*, First and second pairs of antennae (after Knuth).

Scalda, Münst. (*Reckur*, Münst.; *Buria*, Giebel), (Fig. 1383). Cephalothorax ornamented with longitudinal markings, and leaving the last three thoracic segments exposed. Abdomen broad, elongated, and with large surfaces for the attachment of swimming feet, the latter not preserved. The three hindermost abdominal limbs, and the semicircular setigerous telson are developed into a caudal fin. Three species occur in Lithographic Slates of Bavaria.

Order 4. DECAPODA. Latreille.[1]

Cephalothorax completely covered by the carapace, or with but one segment free; five pairs of walking feet, the first two or three pairs usually chelate. Test prolonged into

(Palaeontogr., XV.), 1868.—*Knuth*, A., Ueber wenig bekannte Crustaceen von Solenhofen (Zeitschr. deutsch. geol. Ges., XXII.), 1870.—*Woodward*, H., Contributions to the Knowledge of Fossil Crustacea (Quar. Journ. Geol. Soc., XXXV.), 1879.

[1] Literature:

Münster, G. Graf zu, Ueber die fossilen langschwänzigen Krebse in den Kalkschiefern von Bayern (Beitr. z. Petrefaktenkunde, Heft. II.), 1839.—*Meyer, H. von*, Neue Gattungen fossiler Krebse, etc., Stuttgart, 1840.—Jurassische und triasische Crustaceen (Palaeontogr., IV. p. 44), 1854.—Die Prosoponiden (*ibid.* VII.), 1860.—Tertiäre Decapoden aus den Alpen, etc. (*ibid.* X.), 1862.—*Reuss, A. E.*, Zur Kenntniss fossiler Krabben (Denkschr. Akad. Wiss. Wien., XVII.), 1857.—Ueber fossile Krebse aus den Raibler Schichten (Beitr. z. Palaeont. Oesterreichs, I.), 1858.—*Bell, T.*, Monograph of the Fossil Malacostracous Crustacea of Great Britain (Palaeont. Soc., 1857-62).—*Étallon, A.*, Description des Crustacés fossiles (Bull. Soc. Geol. France [2], XVI.), 1859.—*Oppel, A.*, Ueber jurassische Crustaceen (Palaeont. Mittheil. Museum Bay. Staates I.), 1862.—*von der Mark, W.*, Fossile Fische, Krebse und Pflanzen aus der Kreide (Palaeont., XI.), 1863.—*Idem*, and *Schlüter, C.*, Neue Fische und Krebse aus der Kreide von Westphalen (*ibid.* XV.), 1868.—*Schlüter, C.*, Die Macruren-Decapoden Westphalens (Zeitschr. deutsch. geol. Ges., XIV.), 1862.—Kreide- und Tertiär-Krebse des nördlichen Deutschlands (*ibid.* XXXI.), 1879.—*Stimpson, W.*, Fossil Crab from Gay Head (Journ.

a frontal spine (rostrum) between the compound pedunculate eyes. Gills borne on or near the basal joints of maxillipeds and legs, and enclosed in a branchial chamber formed by a downward expansion of the carapace on either side.

No Palaeozoic Crustacean is known which displays typical Decapod characters, and it is possible the group did not become differentiated until the Trias, where the first undoubted remains occur. Their forerunners, however, are evidently to be sought for amongst the collective forms already cited under the *Schizopoda*. Although a division into the sub-orders *Macrura* and *Brachyura* is not strictly natural, yet it is of certain convenience to the palaeontologist. The so-called *Anomura*, which are very rare in the fossil state, are distributed between these two sub-orders.

Sub-Order A. MACRURA. Latreille. (Lobsters, Shrimps, Prawns.)

Abdomen strongly developed, as long or longer than the cephalothorax, and never inflexed beneath the latter; it is provided with four to five pairs of abdominal feet, and the swimmerets of the sixth segment form with the telson a strong caudal fin. The third pair of maxillipeds are long and slender, and do not completely cover the preceding ones.

(1) The family *Caridida*e or prawns have a usually compressed body covered by a delicate cuticula; legs long and slender, some or all of the pairs chelate; rostrum usually well developed, and large antennal scale present. Undoubted Caridids are represented in the Lithographic Slates of Bavaria by the following genera:—*Penaeus*, Fabr. (Fig. 1384); *Acanthochcirus*, Oppel; *Bylgia*, *Drobna*, *Dusa*, *Aeger* (Fig. 1385), *Blaculla*, *Udora*, *Hefriga*, *Elder*, Münster; and *Udorella*, Oppel. *Pseudocrangon*, Schlüter, and *Oplophorus*, Milne-Edw., occur in the Upper Cretaceous of Westphalia. *Homelys*, v. Meyer, and *Palaemon*, Fabr., are Tertiary genera, the latter also Recent.

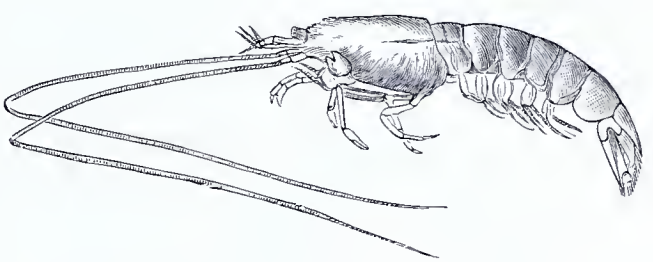


Fig. 1384.

Penaeus Meyeri, Oppel. Lithographic Slates; Solenhofen. 1/2.

(2) The *Eryonidae* have a thin, broad, and depressed carapace, with a median longitudinal keel; antennal scale small; four anterior pairs of feet chelate; caudal fin large. *Tetrachela*, Reuss, from the Upper Trias of Raibl, is one of the oldest known Decapods. *Eryon*, Desm. (Fig. 1386), ranges from the Lias to Cretaceous, exquisite examples being found in the Lithographic Slates. *Polycheles*, Heller, and *Willemoesia*, Grote, are recent deep-sea forms.

(3) In the *Palinuridae* (*Loricata*) the body is stout, antennal scale small, and all

Boston Soc. Nat. Hist., VII.), 1863.—*Fritsch*, *A.*, Ueber die Callianassen der böhmischen Kreide (Abhandl. Böhm. Ges. Wiss. [6], I.), 1868.—*Carter*, *J.*, On Orithopsis Bonneyi (Geol. Mag. [1], IX.), 1872.—Decapod Crustaceans of the Oxford Clay (Quar. Journ. Geol. Soc., XLII.), 1886.—(*Ibid.* LIV.), 1898.—*Woodward*, *H.*, Macrurous Crustacea, etc. (*ibid.* XXIX., XXXII.), 1872-76.—*Tribolet*, *M.*, Descriptions des Crustacés du terrain neocomien (Bull. Soc. Geol. France [3], II., III.), 1874-75.—*Bittner*, *A.*, Brachyureu des vicentischen Tertiärgebirges (Denkschr. Akad. Wiss. Wien., XXXIV., XLVI.), 1877-83.—*Winkler*, *T. C.*, Études sur les genres Pemphix, Glyphaea, et Araeosternus (Archiv. Museé Tyler [2], I.), 1883.—*Ortmann*, *A. E.*, Das System der Decapoden-Krebse (Zool. Jahrb. Syst. Abth., IX.), 1896.—On Linuparus in the Upper Cretaceous of Dakota (Amer. Journ. Sci. [4], IV.), 1897.—*Moericke*, *W.*, Die Crustaceen der Stramberger Schichten (Palaeontogr. Suppl., II.), 1897.—*Lörenthey*, *E.*, Ueber die Brachyuren der pal. Sammlung des Bayerischen Staates (Termeszetrajki Füzetek Budapest, XXI.), 1898.—Beitrag zur Decapodenfauna des ungärischen Tertiars (*ibid.*; also in Math.-naturw. Ber. aus Ungarn XIV.), 1898.

the feet non-chelate. Carapace very thick and rigid, its frontal portion always united

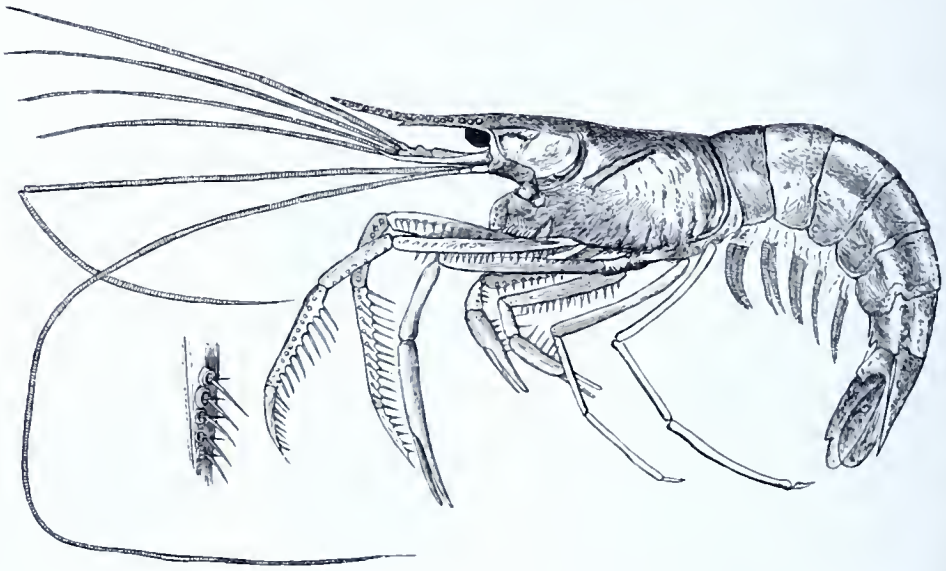


Fig. 1385.

Aeger tipularius, Schloth. sp. Lithographic Slates; Eichstadt, Bavaria. 2/3.

with the segment of the antennulae. The oldest representatives, *Scapheus* and

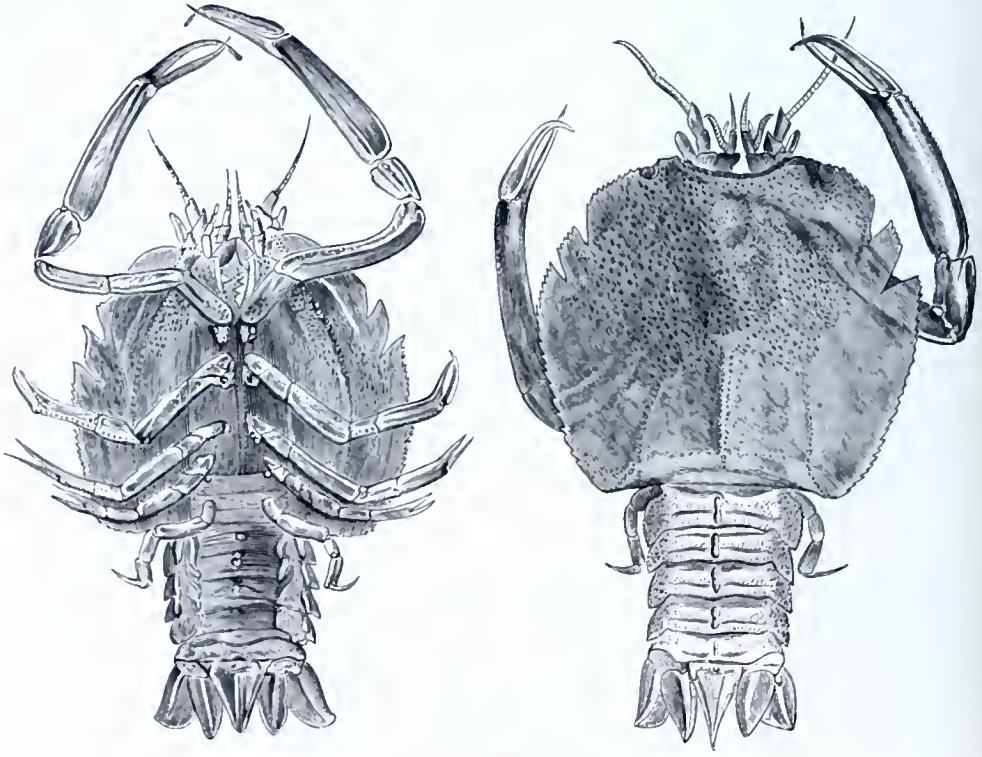


Fig. 1386.

Eryon propinquus, Schloth. sp. Lithographic Slates; Solenhofen, Bavaria. 1/2.

Pracatya, Woodward, are Liassic. *Mecochirus*, Kef. (Fig. 1387), is found in the Middle

and Upper Jura. *Palinurina* and *Cancrinus*, Münster, occur in the Lithographic

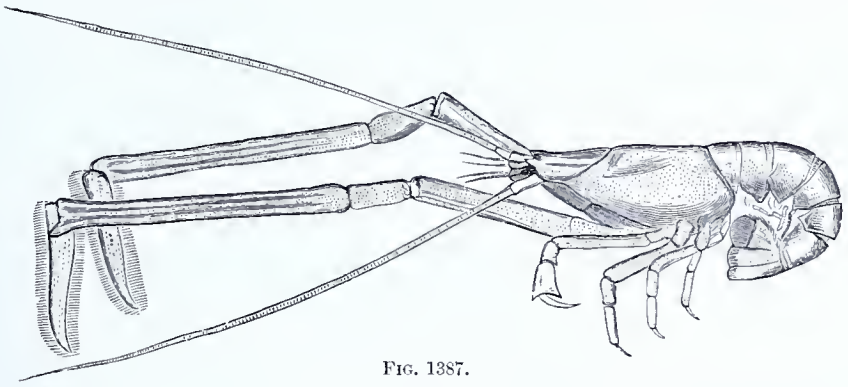


Fig. 1387.

Mecochirus longimanus, Schloth. sp. Lithographic Slates; Eichstädt, Bavaria. 1/2.

Slates. *Palinurus*, Münst., and *Linuparus*, Gray, range from the Upper Cretaceous to Recent.

(4) The family *Scyllaridae* (with the genera *Podocrates*, Becks, and *Eurycarpus*, Schlüter, from the Upper Cretaceous; *Scyllarus*, Fabr., ranging from the latter to Recent; and the Eocene genera *Archaeocarabus*, M'Coy, and *Scyllaridia*, Bell) differs from the *Palinuridae* in having a depressed carapace and lamellate antennae.

(5) The *Glypheidae* contain but one recent genus, *Araeosternus*, de Man, from Sumatra, but have a large series of fossil forms. The family resembles the *Palinuridae* in structure of appendages, but in all

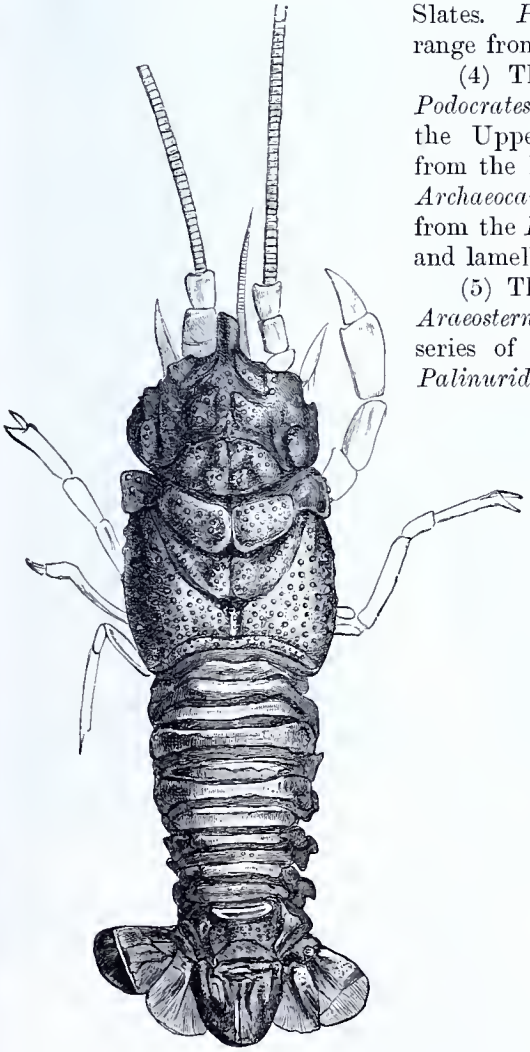


Fig. 1388.

Pemphix Sueurii, Desm. Muschelkalk; Crailsheim, Würtemberg. 1/1.

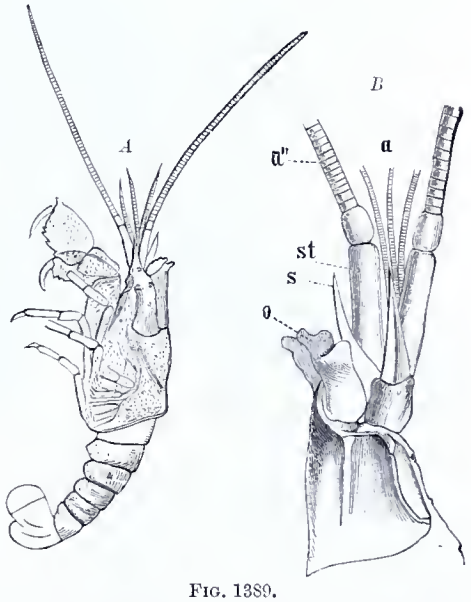


Fig. 1389.

Glyphaea tenuis, Opp. Lithographic Slates; Eichstädt, Bavaria. *A*, Side-view, 1/1. *B*, Rostral region enlarged. *a*, *a''*, First and second pairs of antennae; *o*, Eye; *s*, Antennal scale; *st*, Base of second pair of antennae.

other respects approaches the *Astacidae*. Carapace solid and roughened, cervical suture deep; sternum narrow; legs monodactyle, the first pair being the largest, and in some cases sub-chelate. *Pemphix*, v. Meyer (Fig. 1388), occurs in the Muschelkalk; *Lithogaster* and *Glyphaea*, v. Meyer (Fig. 1389), range from the Trias to Cretaceous; *Pseudoglyphaea*, Oppel, is Jurassic; and *Meyeria*, M'Coy, Neocomian.

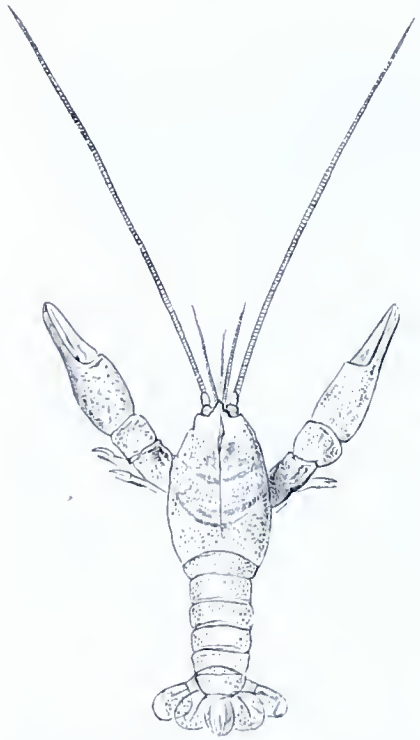


Fig. 1390.

Eryma leptodactylina, Germ. sp. Lithographic Slates; Solenhofen, Bavaria. 1/1 (after Oppel).

(6) The *Astacidae* are distinguished by the possession of a narrow sternum; chelate appendages, of which the first pair is very strongly developed, and an antennal scale. Both salt- and fresh-water forms occur. *Eryma*, v. Meyer (Fig. 1390), *Pseudastacus*, *Stenochirus*, *Etallonia*, Oppel, are found in the Lithographic Slates. Isolated chelae of *Magila* (Fig. 1391) are abundant throughout the Jura. *Enoplocytia*, M'Coy; *Nymphaeops*, Schlüt.; *Hoploparia*, M'Coy; *Oncoparia*, Bosquet; and *Palaeastacus*, Bell, occur in the Upper Cretaceous of Westphalia, Bohemia, and England. *Homarus*, Milne-Edw.; *Nephrops*, Leach; and *Astacus*, Fabr., range from the Upper Cretaceous to Recent.

Fig. 1391.

Magila suprajurensis, Quenst. sp. Upper Jura; Sedlingen, Wurtemberg. Chela.

(7) The *Thalassinidae* have the abdomen much elongated, carapace with two longitudinal sutures, anterior feet the largest and chelate, and whole body except the chelae enclosed in a thin integument. Numerous chelae referable to *Callianassa*, Leach (Figs. 1392, 1393), are found in the Cretaceous and Tertiary. *Thalassina*, Latr., is Tertiary and Recent.

(8) The *Galatheidae* differ from the last family in having the broad abdomen slightly recurved below; cephalothorax strongly calcified and with numerous transverse

Fig. 1392.

Callianassa Archiaci, M.-Edw. Turonian; Montdragon, Var. (after Milne-Edwards).

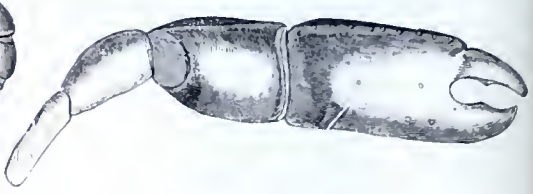


Fig. 1393.

Callianassa antiqua, Otto. Turonian; Turnau, Bohemia. Right chela.

furrows; posterior pair of feet very small and delicate. Fossils are extremely rare, and consist only of chelae of *Galathea* from the Upper Cretaceous of Faxoe. Equally rare are the chelae of *Pagurus*, belonging to the *Paguridae* or Hermit Crabs, described from the Eocene of Hungary.

Sub-Order B. BRACHYURA. Latreille. (Crabs.)

Abdomen short and reduced, without caudal fin, and curved around against the excavated ventral surface of the cephalothorax; in the male narrow and pointed, with one to two pairs of abdominal feet; in the female broad, with four pairs. Carapace frequently broader than long, usually depressed; antennae short; third pair of maxillipeds completely covering the mouth parts.

(1) The *Dromiacea* (*Notopoda*) have the carapace sub-triangular, sub-quadrate, or sub-orbicular, and the fifth pair of feet, which are sometimes chelate, are carried dorsally. *Prosopon*, v. Meyer (Fig. 1394),

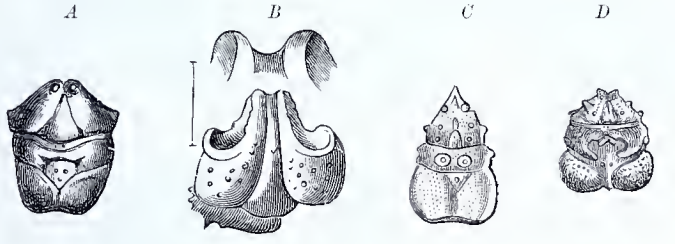


Fig. 1394.

A, *Prosopon marginatum*, v. Meyer. Upper Jura (ε); Oerlinger Valley, near Ulm. 3/2. *B*, *P. personatum*. Upper Jura (γ); Weissingen, Würtemberg. Rostrum enlarged. *C*, *P. aculeatum*, v. Meyer. Same locality as *A* and *D*. *D*, *P. pustulatum*, Quenst.

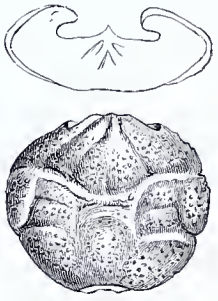


Fig. 1395.

Dromiopsis rugosa, Schloth. sp. Uppermost Cretaceous; Faxoe, Denmark.

appears in the Lower Oolite, is abundant in the Upper Jura, and persists into the Neocomian. Similar, but somewhat larger forms with broader carapace occur in the

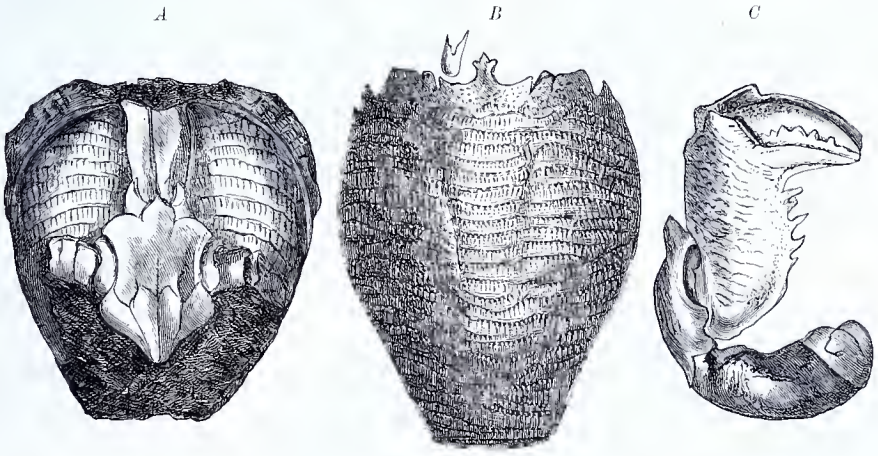


Fig. 1396.

A, *B*, *Ranina Marestiana*, König (= *R. Helli*, Schafh.). Eocene; Kressenberg, Bavaria. Ventral and dorsal views. *C*, Chela of *R. Bouilleana*, M.-Edw. Eocene; Biarritz, France. 1/2.

Upper Cretaceous. Such are *Dromiopsis*, Reuss (Fig. 1395); *Binkhorstia*, Noetling; and *Polyenedium*, Reuss.

(2) The *Raninoidea* have the carapace somewhat elongate, broadest and truncate in front, chelae strongly compressed, and the other feet flattened and natatory. *Raniella* and *Raninoides*, Milne-Edw., occur in the Upper Cretaceous. *Ranina*, Lam. (Fig. 1396), ranges from Eocene to Recent.

(3) The *Oxystomata* have a rounded cephalothorax with the frontal region not projecting. The external maxillipeds together have a triangular outline, their apices

being just behind the excurrent gill opening. *Palaeocorystes*, Bell (Fig. 1397), ranges from the Gault to Eocene. *Eucorystes* and *Necrocarcinus*, Bell (Fig. 1398), are Cretaceous; *Hepatiscus*, Bittner, is Eocene; *Calappa* and *Matuta*, Fabr., range from Eocene to Recent.

Fig. 1397.

Palaeocorystes Stokesi, Mant. sp. Upper Greensand; Cambridge, England.

Fig. 1398.

Necrocarcinus tricarinatus, Bell. Greensand; Cambridge, England (after Bell).

Fig. 1399.

Micromaia tuberculata, Bittner. Eocene; San Giovanni Illariene, Italy (after Bittner).

(4) In the *Oxyrhyncha*, or triangular crabs, the cephalothorax is broad behind, pointed in front, and the external maxillipeds (buccal frame) are quadrilateral in outline. Fossil forms few and small. *Micromaia*, Bittner (Fig. 1399), and *Microthorax*, Noetling, are Eocene and Miocene respectively. *Lambrus*, Leach, is Eocene and Recent.

(5) The *Cyclometopa* (*Cancroidea*) have a broad carapace, arcuate in front and narrowed behind, without prominent rostrum. The tribe is subdivided into the swimming crabs (*Portunidae*) and shore crabs (*Cancridae*), the former being distinguished by their lamellate feet, the fifth pair terminating in a broad flattened paddle. To the first group belong *Neptunus* and *Achelous*, de Haan; *Charybdis*, Dana; *Portunites*, Bell; *Psammocarcinus*, M.-Edw. (Fig. 1400), etc., which make their appearance in the Eocene. The *Cancridae* are older; *Palaeocarpilius*, M.-Edw., appearing in the Upper Cretaceous and Eocene; and *Panopaeus*, M.-Edw., ranging from Cretaceous to Recent. *Harpactocarcinus*, M.-Edw.; *Lobocarcinus*, Reuss (Fig. 1401); *Xanthopsis*, M'Coy (Figs. 1402, 1403), are very abundant in the Eocene; *Atergatis*, de Haan, in the Oligocene; *Xantho* and *Cancer*, Leach, in the Neocene. *Neptocarcinus* and *Carcinocarcinus*, Lörenthey, are described from the Eocene of Hungary and Bavaria respectively.

Fig. 1400.

Psammocarcinus Hericarti, Desm. sp. Middle Meeressand (Miocene); Le Gué-à-Tresmes, France (after A. Milne-Edwards).

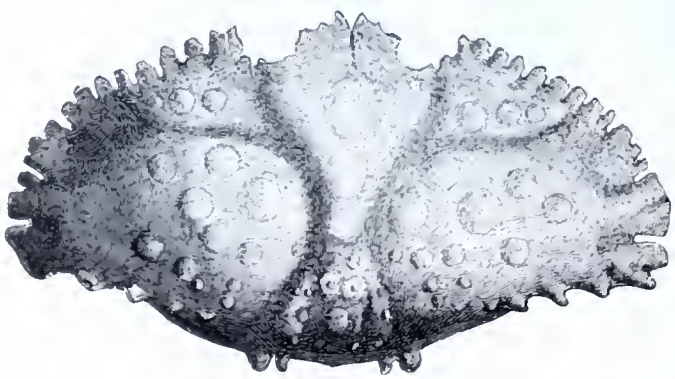


Fig. 1401.

Lobocarcinus Paulino-Würtembergicus, v. Meyer. Eocene; Mokkatam, near Cairo, Egypt. Male.

(6) The *Catometopa* have the carapace quadrilateral in outline, the front being abruptly truncated or slightly arcuate, and the sides nearly straight and converging behind. Living species are marine, fluviatile, or terrestrial. *Galenopsis*, *Coeloma*, M.-Edw. (Fig. 1404); *Litoricola*, Woodw.; and *Palaeograpsus*,

Bittner, are known from the Eocene and Oligocene. The recent *Thelphusa*,

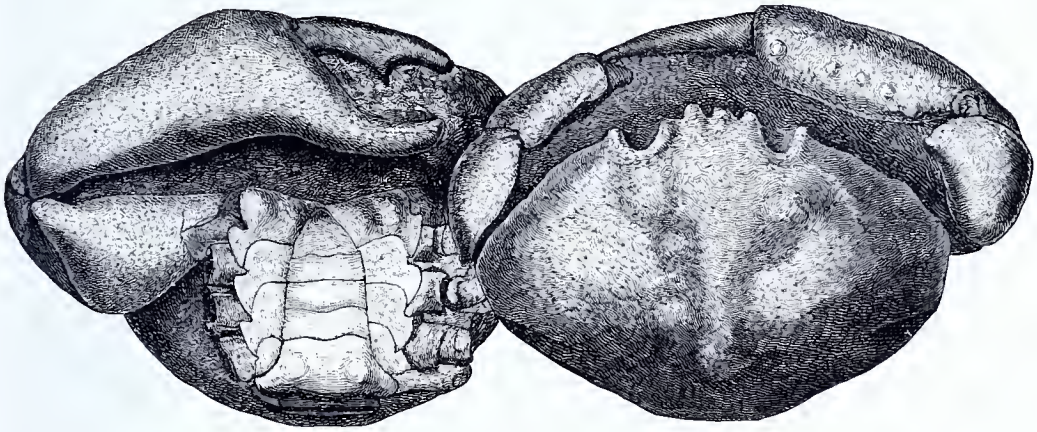


Fig. 1024.

Xanthopsis Kressenbergensis, v. Meyer. Eocene; Kressenberg, Bavaria. Male, ventral and dorsal aspects, 1/2.

Latr., and *Gecarcinus*, Leach, occur in the fresh-water Miocene beds of Oeningen

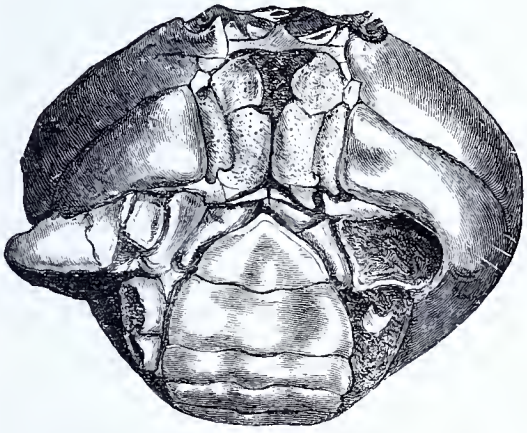


Fig. 1403.

Xanthopsis Bruckmanni, v. Meyer. Eocene; Sonthofen, Bavaria. Ventral view of female, 1/1.

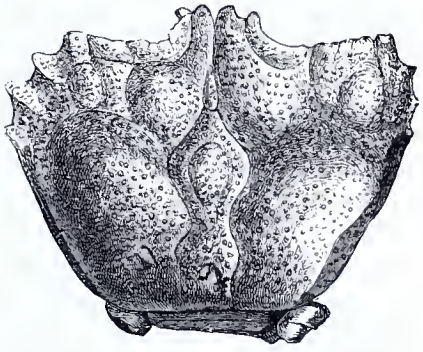


Fig. 1404.

Coeloma vigil, M.-Edw. Eocene; Laverda, Italy.

and Engelwies in Baden. *Archaeoplax*, Stimpson, is found in the Miocene of Gay Head, Massachusetts.

Order 5. EDRIOPHTHALMA. Leach.

(*Arthrostraca*, Burmeister; *Tetradecapoda*, Dana.)

Malacostraca with lateral sessile eyes, usually with seven, more rarely six or fewer free cephalothoracic segments, and an equal number of pairs of legs adapted for creeping or swimming.

Sessile-eyed *Crustacea* are somewhat rare in the fossil state, and as a rule are imperfectly preserved; this, taken in connection with the fact that the classification is largely based upon the minute mouth-parts, makes the identification and systematic arrangement very difficult and often impossible.

Sub-Order A. AMPHIPODA. Latreille.

Body laterally compressed, with gills borne on the bases of the walking feet; abdomen elongate, the three anterior feet natatory, the rest posteriorly directed and saltatory.

The Amphipods, or beach fleas, are mostly small, aquatic animals, and generally marine. They live in shallow water between rocks, beneath seaweed, etc., or in some cases in tubes or burrows constructed by themselves. They leave tracks upon the surface of mud and sand which resemble the Palaeozoic *Nereites*. Fossil remains are extremely scarce, and are derived chiefly from fresh-water strata.

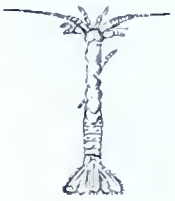


Fig. 1405.

Palaeorchestia parallela, Fritsch sp. Coal Measures; Lisek, near Beraun, Bohemia. 1/1 (after Fritsch).

A few Palaeozoic forms have been described under the names of *Necrogammarus Salweyi*, Woodw., from the Ludlow beds; *Diplostylus Dawsoni*, Salter, from the Carboniferous of Nova Scotia; *Palaeorchestia*, Zitt. (Fig. 1405), from the Coal Measures; and *Bostrichopus*, Goldf., from the Culm Measures of Herborn. These are all problematical forms of doubtful relationships. Less uncertain in its position is *Acanthotelson*, Meek and W., from the Carboniferous of Illinois, which, although raised by Packard to ordinal rank (*Syncarida*, see above under *Schizopoda*), shows no features incompatible with Amphipod relations. The few Tertiary forms, such as *Gammarus*, Fabr. (Fig. 1406); *Typhis*, Risso; and *Palaeogammarus*, Zadd., closely resemble living types.

Fig. 1406.

Gammarus Oeningensis, Heer. Miocene; Oeningen, Baden. 2/1.

Sub-Order B. ISOPODA. Latreille.[1]

Body depressed, usually broad, flat below, rounded above; with seven free thoracic segments, and no strongly developed carapace. Gills borne on the lamellar appendages of the abdomen, which is short-ringed and often reduced, its segments partially fused. Caudal segment relatively large, shield-shaped.

Fig. 1407.

Urda rostrata, Munst. Lithographic Slates; Solenhofen, Bavaria. 1/1 (after Kunth).

Most Isopods are marine, frequenting the coast; a few inhabit fresh water, and about an equal number (*Oniscidae*) live in moist terrestrial localities. Of the somewhat rare fossil remains, *Praearcturus*, Woodward, is a large form from the Old Red Sandstone of Herefordshire; *Amphipeltis paradoxus*, Salter, occurs in the Devonian of Nova Scotia; *Arthropleura*, Jordan, is found in the Coal Measures; *Urda*, Münster (Fig. 1407), in the Lithographic Slates; *Archaeoniscus*, M.-Edw. (Fig. 1408), in the English Purbeck;

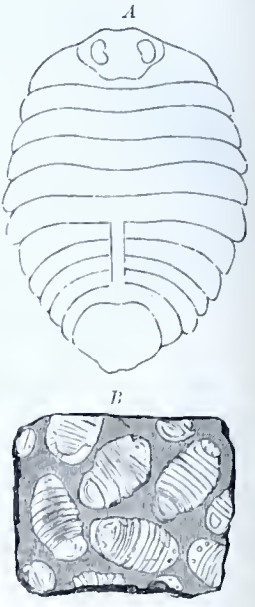


Fig. 1408.

A, *Archaeoniscus Brodei*, M.-Edw. Purbeck; Vale of Wardour, Wiltshire. 3/1 (after Woodward). *B*, Fragment of matrix, 1/1 (after Quenstedt).

[1] Literature:

Milne-Edwards, H., Sur deux crustacés fossiles (Ann. Sci. Nat. Zool. [2], XX.), 1843.—On Archaeoniscus (Ann. Mag. Nat. Hist. [2], XIII.), 1844.—*Meyer, H. v.*, Ueber Palaeoniscus obtusus Palaeontogr., V.), 1858.—*Kauth, A.*, Crustaceen von Solenhofen (Zeitschr. deutsch. geol. Ges., XXII.), 1870.—*Woodward, H.*, Several papers on British Fossil Isopods in Trans. Woolhope Field Club, 1870; Geol. Mag., VII., 1870; [3], VII., 1890; [4], V., 1898; and Quar. Journ. Geol. Soc., XXXV., 1879.—*Ammon, L. v.*, Beitrag zur Kenntniss der fossilen Asseln (Sitzungsber. Bayer. Akad. Wiss.), 1882.—*Carter, J.*, On Fossil Isopods (Geol. Mag. [3], VI.), 1889.

Cyclosphaeroma, Woodw., in the Great Oolite and Purbeck; *Palaega*, Woodw. (Fig. 1409), in the brackish water marls (Oligocene) of Paris and the Isle of Wight. *Eosphaeroma*, Woodw. (Fig. 1410), and several Oniscids are found in the Miocene of Oeningen, Baden, and in amber.

[The different orders of *Malacostraca*, with the exception of the Phyllocarids, have been revised by Professor J. S. Kingsley, of Tufts College, Massachusetts. He has also drawn up the diagnoses of the larger groups of Arthropods, and the entire MS. for this phylum has received the benefit of his expert criticism.—TRANS.]

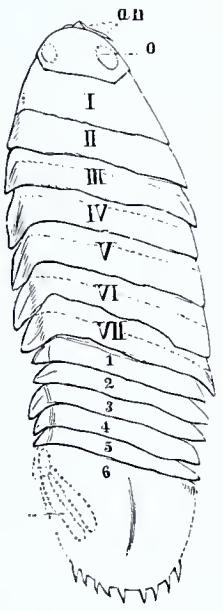


FIG. 1409.

Palaega scrobiculata, v. Ammon. Lower Oligocene; Häring, Tyrol. *an*, Antennae; *o*, Eyes; p^6, Hindermost swimming-foot; I—VII, Thoracic segments; 1—6, Abdominal segments.

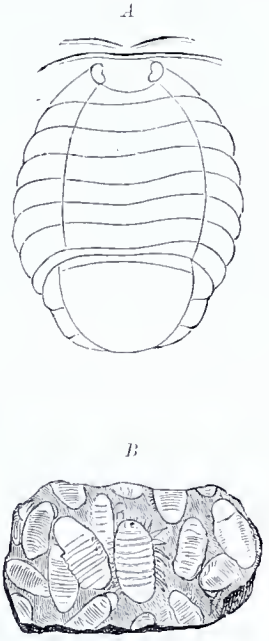


FIG. 1410.

A, *Eosphaeroma Brongniarti*, M.-Edw. Middle Oligocene; Butte de Chaumont, near Paris. $^3/_1$ (after Woodward). *B*, Fragment of matrix, $^1/_1$ (after Quenstedt).

Class 2. ACERATA. Kingsley.

Primitively branchiate Arthropods in which the branchial folds function as gills or as lungs, or become metamorphosed into air-tubes (tracheae) penetrating the body. The body is divided into two regions, cephalothorax and abdomen, the line between the two passing behind the sixth pair of appendages. Cephalothoracic segments usually coalesced, those of the abdomen either free or fused. Frequently a post-anal spine is present. Antennae lacking; genital openings upon the first abdominal somite; midgut long; spermatozoa motile; development without nauplius or zoea stages.

The sole living representative of this group, *Limulus*, has long been regarded as occupying a peculiarly isolated position among *Crustacea*. Its Arachnidian affinities were long ago pointed out by Straus-Dürckheim, and additional reasons for removing the Merostomes from association with the *Crustacea* have been brought forward by later writers, among whom may be mentioned H. and A. Milne-Edwards, Dohrn, Lankester, van Beneden, Kingsley, and Laurie.

The points most relied upon for the association of *Merostomata* and *Arachnida* are: (1) the numerical homologies of the segments and appendages; (2) the exact homologies existing in the respiratory organs; (3) the fact that the cephalothoracic appendages are pediform, the basal joints serving as jaws; (4) the presence of true nephridia opening in the base of the third or fifth pair of appendages, or in both; (5) genital openings in the seventh (or more probably eighth) segment of the body; (6) extreme length of the midgut; (7) presence of an internal structure, the *entosternite*; (8) inclusion of the ventral nerve cord and its nerves in the sternal artery and its branches; (9) the close similarities in the central nervous system (Kingsley).

The *Acerata* are divided into two groups—*Merostomata* and *Arachnida*.

Sub-Class 1. MEROSTOMATA. (Dana.) Woodward.[1]

Six pairs of ambulatory limbs about the mouth, the first of which in some, if not in all, cases terminate in chelicerae. The rest serve as organs of locomotion, and their coxal

[1] The best bibliographies of *Merostomata*, including also historical reviews of the group, are to be found in the following memoirs:—*Woodward, H.*, A Monograph of the British Fossil Crustacea of the Order Merostomata (Palaeont. Soc. pp. 21-30), 1866-78.—*Packard, A. S.*, On the Carboniferous Xiphosurous Fauna of North America (Mem. Nat. Acad. Sci. III. pp. 153-156), 1885.

joints for prehension and mastication. Behind the mouth is a single or paired metastoma. Cephalothorax depressed, with usually a pair each of median ocelli and lateral compound eyes. Respiration by means of lamellate branchiae ("gill-books") borne on appendages two to six of the abdomen, and protected by the enlarged first pair (operculum) which covers them. In Limulus there are no salivary glands, no Malpighian tubules, and no embryonic membranes ("amnion") are found in development.

The prevailing modern opinion is that the body is divided into two regions only (cephalothorax and abdomen) instead of into three (head-shield, "thorax," and abdomen), as a number of earlier writers have maintained. According to the latter interpretation, the abdomen of *Limulus* is represented merely by the telson, but in Eurypterids by a variable number of segments.

Order 1. XIPHOSURA. Gronovius.[1]

Body, in mature types, distinctly trilobed longitudinally. Cephalothorax large, semicircular, the compound eyes laterally situated, and ocelli in the centre in front. First pair of appendages chelicerate. Metastoma with two small accessory plates. Abdomen with seven to ten segments, which are dorsally free or coalesced; the six anterior ones provided with lamellar appendages on the under side. Telson long, ensiform, movable.

Fig. 1411.

Cyclus americanus, Pack. Coal Measures; Mazon Creek, Illinois. Showing traces of legs and alimentary canal. 1/1.

Family 1. **Cyclidae.** Packard.

Cephalothorax small, orbicular, discoidal or convex, calcareous or chitinous, bounded by a distinct border. Appendages nearly as in embryonic Limulus.

Cyclus, de Kon. (Fig. 1411). Known almost solely by the cephalothorax with its imperfectly preserved appendages, which seem to be simple swimming legs. Their enlarged joints cover the ventral surface of the carapace everywhere except in the centre, which is occupied by a V-shaped plate, towards the pointed extremity of which all the basal joints of the limbs converge. Coal Measures; Great Britain and Illinois.

Some of the described species are apparently larval *Eurypterus*, *Stylonurus*, *Prestwichia*, etc.

[1] Literature:

Hoeven, J. van der, Recherches sur l'histoire naturelle et l'anatomie des Limules. Leyden, 1838.—*Münster, G. Graf zu*, Beiträge zur Petrefaktenkunde, Hefte I., III., 1840.—*Gegenbaur, C.*, Anatomische Untersuchungen eines Limulus (Abhandl. naturf. Ges. Halle, IV.), 1858.—*Baily, W. H.*, Explanation of Sheet 137 of the Maps of the Geol. Surv. Scotland, 1859.—Remarks on Belinurus (Ann. Mag. Nat. Hist. [3], XI.), 1863.—*Giebel, C. G.*, Limulus Deeheni (Zeitschr. gesammt. Naturw. XXI.), 1863.—*Meek, F. B.*, and *Worthen, A. H.*, Report Geol. Surv. Illinois, vol. III. p. 547, 1868.—*Woodward, H.*, On Neolimulus (Geol. Mag., V.), 1868.—On the Genus Cyclus (*ibid.* VII. p. 554; also [4], I. p. 530), 1870-94.—Notes on Merostomata (*ibid.* IX.), 1872.—*Dohrn, A.*, Embryologie und Morphologie des Limulus (Jenaische Zeitschr., VI.), 1871.—*Packard, A. S.*, Development of Limulus (Mem. Boston Soc. Nat. Hist., I.), 1872.—Anatomy, Histology, and Embryology of Limulus (Anniv. Mem. Boston Soc. Nat. Hist.), 1880.—Carboniferous Xiphosurous Fauna of North America (Mem. Nat. Acad. Sci., III.), 1885.—*Milne-Edwards, A.*, Recherches sur l'anatomie des Limulus (Ann. Sci. Natur. Zool. [5], XVII.), 1873.—*Lankester, E. R.*, Limulus an Arachnid (Quar. Journ. Microsc. Soc., XXI.), 1881.—*Peach, B. N.*, Further Researches among Crustacea and Arachnida (Trans. Roy. Soc., Edinburgh, XXX.), 1882.—*Williams, H. S.*, New Limuloid Crustacean from the Devonian (Amer. Journ. Sci. [3], XXX.), 1885.—*Hall, J.*, and *Clarke, J. M.*, Palaeontology of New York, VII. p. 153, 1888.—*Kishenouye, K.*, Development of Limulus (Journ. Coll. Sci. Tokyo, V.), 1891.—*Kingsley, J. S.*, Embryology of Limulus (Journ. Morphol., VII., VIII.), 1892-93.

Family 2. **Belinuridae.** Packard.

Body limuloid in general aspect. Cephalothorax with long, slender genal spines; its appendages as in larval Limulus. Abdomen with the segments distinct; telson long or short.

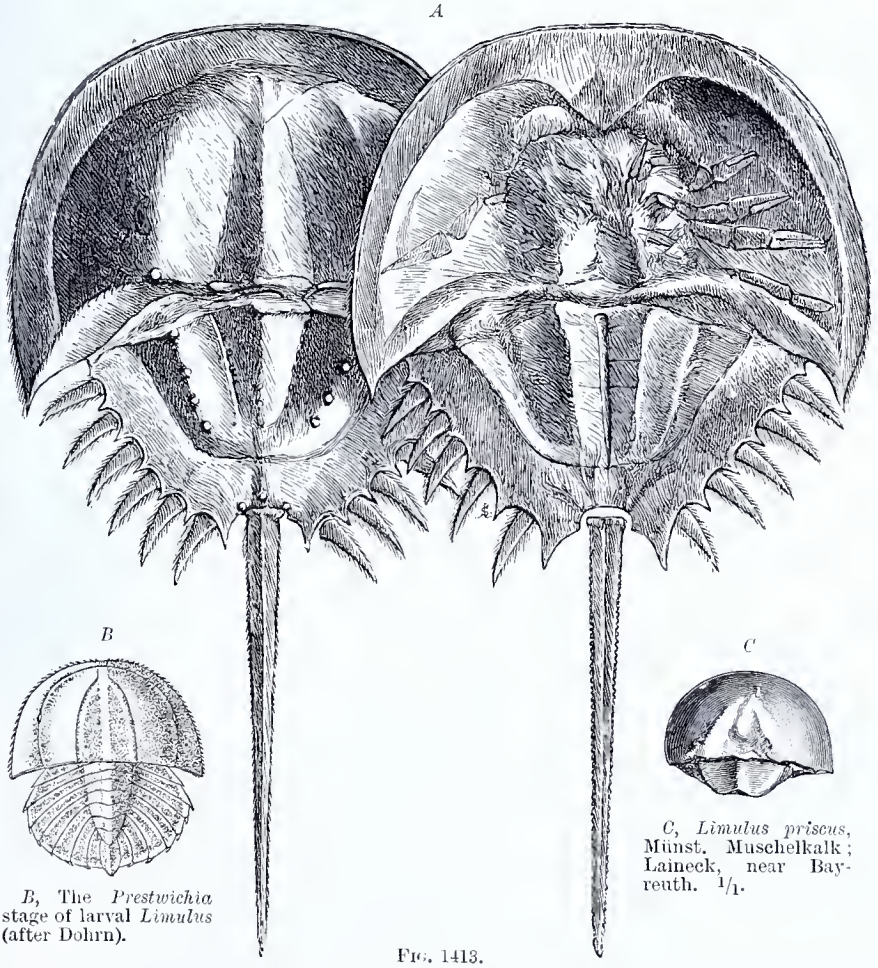
Belinurus, König. (Fig. 1412). Cephalothorax horseshoe-shaped; its central portion sub-quadrate and surrounded by a broad, flat, marginal area. Abdomen with eight segments, besides the very long, slender caudal spine; segments seven and eight are consolidated. Coal Measures; Europe and Illinois.

Prestwichia, Woodw. (*Euproöps*, M. and W.). Differs from *Belinurus* in having seven abdominal segments besides a short caudal spine. Coal Measures; Europe and Illinois.

Protolimulus, Pack. Cephalothorax large, with small appendages; its genal angles less produced than in preceding genera. Abdomen with six segments besides a large, thick caudal spine. Upper Devonian; Pennsylvania.

Fig. 1412.

Belinurus reginae, Baily. Coal Measures; Queen's County, Ireland. $^1/_1$ (after Woodward).



B, The *Prestwichia* stage of larval *Limulus* (after Dohrn).

C, *Limulus priscus*, Münst. Muschelkalk; Laineck, near Bayreuth. $^1/_1$.

Fig. 1413.

A, *Limulus Walchi*, Desm. Lithographic Slates: Solenhofen, Bavaria. Dorsal and ventral aspects, the latter with legs partially preserved. Original in Munich Museum. $^1/_2$.

Family 3. **Limulidae.** Zittel. (King or Horseshoe Crabs.)

Body longer than broad; cephalothorax arched dorsally, the central portion separated from the sides by longitudinal grooves; marginal area large and flat. Abdomen composed of six consolidated segments forming a simple sub-triangular shield, and a long slender telson. Six pairs of abdominal limbs, five of them having over a hundred pairs of gill-leaves.

Limulus, Müller (Fig. 1413). Living species belonging to this, the only genus of the family, occur on the eastern shores of America and Asia. The four cephalothoracic feet are chelate, the sixth pair furnished with a whorl of plates used in pushing the animal through the mud. Gills are borne upon the five posterior pairs of abdominal appendages, the anterior pair being without gills, but having the genital opening upon the posterior face. A small species of *Limulus* occurs in the Buntersandstein of the Vosges. *L. Walchi* is abundant in the Lithographic Slates of Bavaria; *L. Decheni* is found in the Oligocene brown coal of Teuchern, near Merseburg.

Order 2. SYNXIPHOSURA. Packard.

Body elongated; cephalothorax semicircular with the median portion more or less distinctly defined. Compound eyes present in some forms, ocelli not observed except in Neolimulus. Abdomen distinctly trilobed, its segments free, the pleurae flat and extended, and (except in Bunodes) terminating in lateral projections or spines.

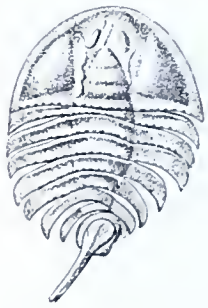


Fig. 1414.

Aglaspis Eatoni, Whitf. Upper Cambrian; Lodi, Wisconsin. $\frac{3}{1}$.

With the exception of the Cambrian *Aglaspis*, all the genera belonging to this order are of Silurian age, and are too imperfectly known as yet to permit a satisfactory grouping into families, although several such have been proposed by Packard. Zittel united them, together with certain genera of *Xiphosura*, in the family *Hemiaspidae*, and this term is retained with the exclusion of the Xiphosurous forms and *Aglaspis*. The latter is without facial sutures.

Family 1. **Aglaspidae.** Clarke.

Cephalothorax moderately large, trilobed; abdominal segments with distinct axis and pleurae; telson long, spiniform.

Aglaspis, Hall (Fig. 1414). Cephalothorax with central portion short and conate, in front of which are approximate compound eyes; bounded on all sides by a distinct border. Abdominal segments not grooved on the pleurae. Cambrian; Wisconsin.

Family 2. **Hemiaspidae.** Zittel.

A somewhat heterogeneous group, separated by at least a family difference from the *Aglaspidae*.

Neolimulus, Woodw. Cephalothorax short and broad, crescentic, elevated mesially, and bearing ocelli. Compound eyes lateral, and connected with the genal angles by a suture. Abdomen very broad, composed of at least nine trilobed segments; telson not observed. This genus connects the *Xiphosura* with the *Synziphosura*. Silurian; Scotland.

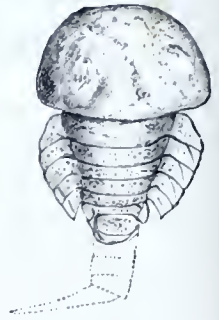


Fig. 1415.

Bunodes lunula, var. *Schrenki*, Nieszk. Silurian; Rootziküll, Oesel. Posterior segments restored from another specimen (after F. Schmidt).

Bunodes, Eichw. (*Exapinurus*, Nieszk.), (Fig. 1415). Cephalothorax semicircular, convex, with radial furrows from the median portion. Eyes wanting, and no genal spines. Facial sutures obscure, converging from the posterior to the anterior margin. Abdomen divided into an anterior portion ("thorax") consisting of six trilobite-like

segments having a broad axis and lamellar pleurae with diagonal pleural lines; and a posterior portion ("abdomen") of four narrow segments, besides a long and acuminate telson. Silurian; Oesel.

Hemiaspis, Woodw. (*Limuloides*, Salter), (Fig. 1416). General form similar to *Bunodes*. Cephalothorax one-half as long as broad, with several genal spines; central portion well defined. Abdomen triangular, with nine segments besides a short telson. Abdominal axis broad, with a median ridge; pleurae short and flat. Silurian; England.

Bunodella, Matthew. Cephalothorax small, abdominal segments seven, acute. Axial portion of the body prominent; telson not observed. Silurian; New Brunswick.

Pseudoniseus, Nieszk. Body oval; cephalothorax short, with broad central portion and large compound eyes; nine trilobed abdominal segments besides a short caudal spine; the posterior ones nearly parallel with the telson. Silurian; Oesel.

Fig. 1416.

Hemiaspis limuloides, Woodw. Silurian; Leintwardine, England. 1/1 (after Woodward).

Order 3. EURYPTERIDA. Burmeister.

(*Gigantostraca*, Haeckel.)[1]

Body elongated, with a thin chitinous epidermal skeleton ornamented by fine scale-like markings. Cephalothorax usually with two large faceted lateral eyes and a pair of median oeelli; on the ventral side with six pairs of legs, of which the first is preoral and chelate. Mouth bordered posteriorly by a metastoma, and anteriorly by an epistoma, both simple plates. Abdomen thirteen-jointed, the anterior six segments bearing ventrally five pairs of broad, leaf-like appendages (apparently comparable to the operculum and branchial appendages of Limulus). The posterior six segments annular, without appendages; telson sometimes spatulate in shape.

This order, which is restricted wholly to the Palaeozoic, embraces the largest Arthropods known, some of them (*Pterygotus*, *Stylonurus*) having attained a length of over 2 metres. The presence of gills upon the branchial appendages shows that in all probability the Eurypterids were aquatic, and the structure of their appendages indicates that they were good swimmers. They are found associated with Graptolites, Cephalopods, and Trilobites in

[1] Literature:

Dekay, J. E., On a Fossil Crustacean (Ann. N.Y. Lyceum Nat. Hist., I.), 1825.—*Roemer F. v.*, Ueber ein Eurypterus (Palaeontogr., I.), 1848.—*M'Coy, F.*, Classification of some British Fossil Crustacea (Ann. Mag. Nat. Hist. [2], IV.), 1849.—*Huxley, T. H.*, On Himantopterus (Quar. Journ. Geol. Soc., XXI.), 1856.—*Idem*, and *Salter, J. W.*, On the Genus Pterygotus (Mem. Geol. Surv. United Kingdom Monogr., I.), 1859.—*Page, D.*, Advanced Text-Book of Geology, 1856 and 1859.—*Nieszkowski, J.*, De Euryptero remipedo. Dorpat, 1858. (Also in Arch. Naturgesch. Liv.-Esth.- und Kurlands, II.), 1859.—*Hall, J.*, Palaeontology of New York, III., 1859.—*Salter, J. W.*, Several Papers in Quar. Journ. Geol. Soc., XIX., 1863.—*Woodward, H.*, Numerous Papers in Geol. Mag., I., 1864; IX., 1872; Quar. Journ. Geol. Soc., XXI., XXIV., XXVII., XXVIII., etc., 1865-72.—*Idem*, Monograph of the British Fossil Crustacea of the Order Merostomata (Palaeont. Soc.), 1866-78.—*Grote, A. R.*, and *Pitt, W. H.*, New Species of Eusarcus and Pterygotus (Bull. Buffalo Soc. Nat. Sci., III.), 1875.—*Pohlman, J.*, Fossils of the Water-Lime Group (*ibid.* IV., V.), 1882-97.—*Peach, B. N.*, Further Researches among Crustacea and Arachnida (Trans. Roy. Soc., Edinburgh, XXX.), 1882.—*Schmidt, F.*, Miscellanea Silurica, III. (Mém. Acad. Imp. Sci., St. Pétersb. [7], XXXI.), 1883.—*Hall, J.*, Second Geol. Surv. Pennsylvania, Rep. PPP. 1884.—*Whiteaves, J. F.*, Palaeozoic Fossils of Canada, III., Pt. 1, 1884.—*Hall, J.*, and *Clarke, J. M.*, Palaeontology of New York, VII., 1888.—*Claypole, E. W.*, On Carcinosoma, etc. (Amer. Geol., VI., XIII.), 1890-94.—*Fraipont, J.*, Eurypterides nouveaux du Dévonien (Ann. Soc. Geol. Belg., XVII.), 1890.—*Laurie, M.*, Eurypterid Remains from Pentland Hills (Trans. Roy. Soc., Edinburgh, XXXVII.), 1892.—Anatomy and Relations of Eurypterida (*ibid.*), XXXVIII.), 1893.—Recent Additions to Knowledge of Eurypterida (Nat. Sci., III.), 1893.—*Whitfield, R. P.*, Report Geol. Survey of Ohio, VII., 1893.—*Holm, G.*, Neue Bearbeitung des Eurypterus Fischeri (Bull. Acad. Imp. Sci., St. Pétersb. [5], IV.), 1896.

the Ordovician of Bohemia and North America; with marine Crustacea (Phyllocarids and Ostracods) in the Silurian; with Ostracoderms and Arthrodites in the Devonian; and with land plants, scorpions, insects, fishes, and fresh-water amphibians in the productive Coal Measures. It is apparent, therefore, that from being originally marine forms, they became gradually adapted to brackish, and possibly even fresh-water conditions. It has been suggested that certain clusters of small roe-shaped bodies may be the ova of *Pterygotus*.

On the under side of the cephalothorax there are five pairs of postoral appendages. These legs consist typically of a basal joint, the inner margin of which is armed with teeth and serves as a jaw, much as in *Limulus* or *Apus*. At the posterior end of the tooth-bearing margin is attached a small oval epicoxite exactly similar to that found in the same place in *Limulus*, and at the anterior angle is attached the long, usually six-jointed ambulatory appendage. The last pair of legs is characterised in all members of the order except *Stylonurus*, by its greater size and usually somewhat flattened form, and ends in an oval plate. This is commonly termed the swimming foot or "paddle," but Lauric has suggested that the animal used it for anchoring or burying itself in the mud.

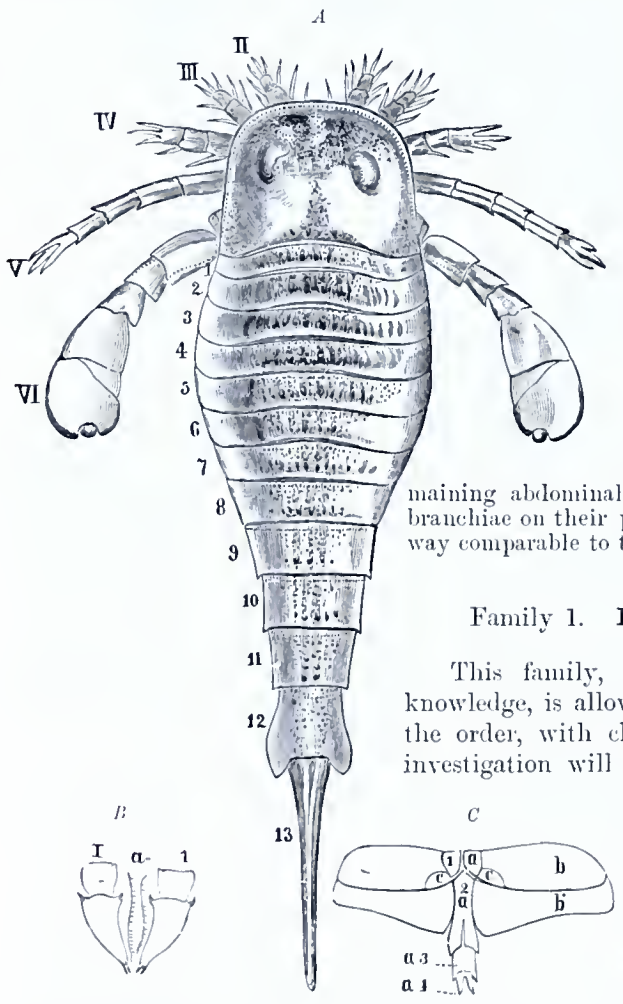


Fig. 1417.

Eurypterus Fischeri, Eichw. Silurian; Rootziküll, Island of Oesel. Restoration after Schmidt. 1/5 natural size. *A*, Dorsal aspect, showing legs II.—VI. beneath the cephalothorax, and 1—13 abdominal segments. *B*, Basipodites of the first pair of legs (*I*); the antennae (*a*) between them now known to be chelicerate. *C*, First lamellar appendage (operculum) of the ventral side, 1/1. *a*, Median process composed of four joints (a^1—4); *b*, Lateral portions; *c*, Triangular piece at the base of the first moiety of the median process (after F. Schmidt).

The ventral surface of the first two abdominal segments is covered by the *genital operculum*, which consists of a pair of plates meeting in the middle line and having a median lobe attached to them; the latter varies in form in the same species, correlating with sex. Underlying the operculum are a number of leaf-like structures, which are almost certainly branchial in function and represent the reduced appendages of the second free segment. The remaining abdominal appendages are plate-like and bear branchiae on their posterior surfaces, being in a general way comparable to those of *Limulus* (Laurie).

Family 1. **Eurypteridae.** Burmeister.

This family, in the present condition of our knowledge, is allowed to embrace all the members of the order, with characters as given above. Future investigation will undoubtedly show reason for the establishment of other families, and some authors have already been disposed to separate *Pterygotus* into a distinct group.

Eurypterus, Dekay (*Lepidoderma*, Reuss; (?) *Campylocephalus*, Eichw.), (Figs. 1417-1421). Body elongate, narrow, attaining sometimes a length of 50 cm. Cephalothorax contained five or six times in total length of the body, depressed convex, sub-quadrate, with rounded anterior angles. Anterior margin nearly straight, posterior slightly concave. Eyes reniform, somewhat in front of the middle; between them and close to the axial line are two ocelli. The entire cephalothorax bordered by a narrow marginal furrow, and the margin broadly enfolded on the ventral side. In the middle of the lower side

is the cleft-shaped mouth, which is bordered laterally by the basal segments of the fifth pair of legs, and posteriorly by the large oval metastoma.

The first pair of appendages were regarded by Woodward and Schmidt as filiform and tactile. Laurie and Holm, however, have found evidence that they are chelicerate, and thus more nearly in accord with homologous structures in other members of the family. The three succeeding appendages are six- or seven-jointed, and covered with fine spines. The fifth pair of legs is eight-jointed, and longer than those in front of it. The posterior pair is a powerful swimming organ; its great sub-quadrate basal joints enclose the metastoma, and together with this, cover nearly one-half of the ventral side of the cephalothorax.

The six anterior abdominal segments together occupy about one-fourth of the body-length. They are short and broad, and nearly uniform in shape; but the second segment has lost its hard skeleton on the ventral surface, and the first covers the greater part of the genital operculum. This first segment joins the posterior margin of the cephalothorax and consists of two lateral

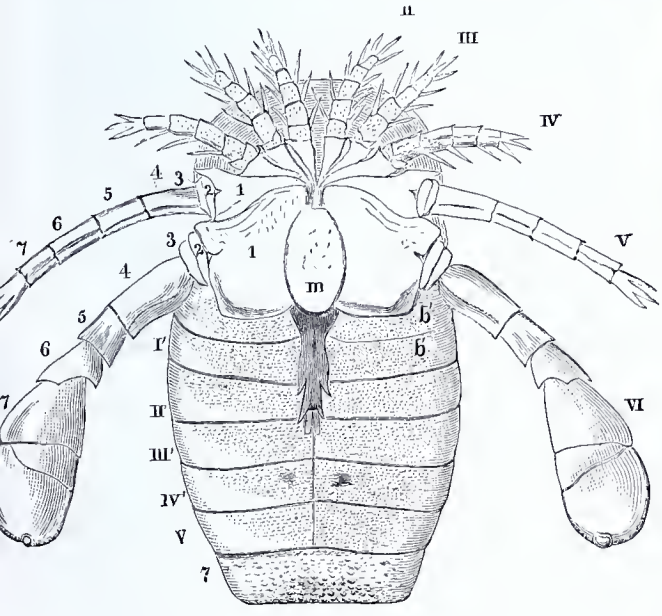


FIG. 1418.

Eurypterus Fischeri, Eichw. Silurian; Rootziküll, Island of Oesel. Ventral aspect. II.—VI., Appendages with the joints numbered. I'.—V'., Lamellar appendages of the under side of abdomen, divided by median suture. I'., First of these, or "operculum," composed of two portions (*b*, *b'*). For abdominal segments after 7 see next figure. $^1/_1$ (after F. Schmidt).

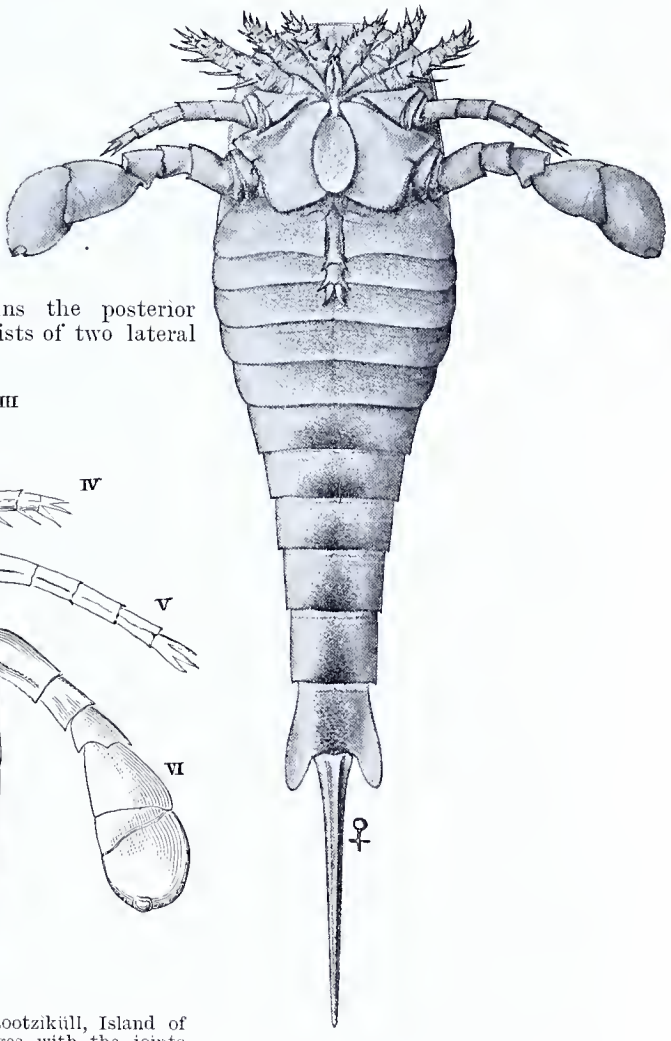


FIG. 1419.

Eurypterus Fischeri, Eichw. Silurian; Island of Oesel. Female individual, $^1/_2$ (from Holm).

portions and a median process. The first six segments are moderately overlapping on the ventral side, and divided by a median suture or cleft into two parts. The following six abdominal segments are ring-like, tapering posteriorly, and the body is terminated by a long slender telson.

About twenty-five species of *Eurypterus* are known, the largest being about 40 cm. long. They are found for the most part in argillaceous or sandy deposits in transition strata between the Silurian and Devonian of England, Gottland, Oesel, Podolia, and in the Waterlime Group of New York. They are rare in the Devonian, but occur again more frequently in the Coal Measures of Scotland, Silesia, Bohemia, Saarbrücken, and Pennsylvania. The last survivor

is from the Permian of Bussaco, Portugal, where it occurs in association with land plants (*Walchia, Sphenopteris*). Type, *E. remipes*, Dekay.

Echinognathus, Walcott. Imperfectly known. Cephalothoracic appendages with numerous curved spines, indicating an animal of large size. Ordovician; New York.

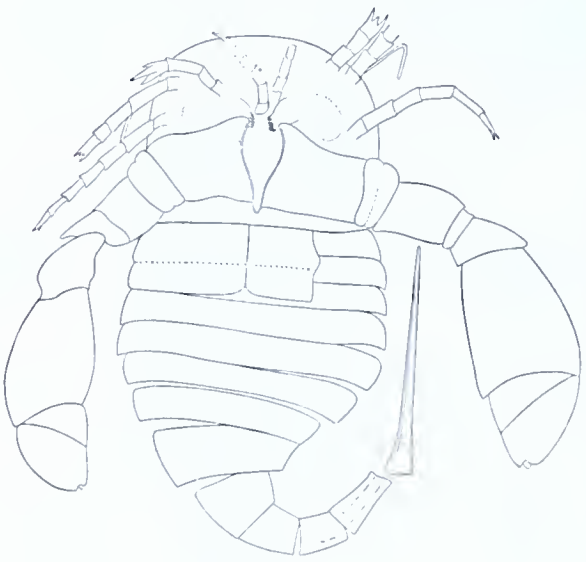


Fig. 1420.

Eurypterus remipes, Dekay. Waterlime (Silurian); Buffalo, New York. Ventral surface of young individual. The first (2nd?) pair of legs, relatively large size and length of swimming feet, and abrupt posterior contraction of abdomen are especially notable. 3/1.

Dolichopterus, Hall. Sixth cephalothoracic leg has the two moieties of the terminal joint subequal in size, and developed as two distinct joints, making nine instead of eight elements in these appendages. Otherwise as in *Eurypterus*. Waterlime (Uppermost Silurian); New York.

Eusarcus, Grote and Pitt (*Drepanopterus*, Laurie; *Eurysoma*, *Carcinosoma*, Claypole). Eurypterids with the first six abdominal segments greatly expanded, those following being abruptly contracted. Terminal joint of the sixth cephalothoracic appendage not expanded. General aspect of body scorpion-like. Silurian; New York, Indiana, Pentland Hills.

Anthraconectes, M. and W. Like *Eurypterus*, but without spines on the joints of the cephalothoracic appendages, and the median process of operculum with two accessory lateral plates. Coal Measures; Illinois.

Adelophthalmus, Jordan and v. Meyer. Eyeless Eurypterids. Coal Measures; Saarbrücken.

Eurypterella, Matthew. Very small, elongated forms. Cephalothorax small, triangular; the first four abdominal segments together sub-quadrate in outline. Surface tuberculated on the posterior edge of the segments. Devonian; New Brunswick.

Fig. 1421.

Eurypterus remipes, Dekay. Waterlime; Buffalo, New York. Very young individual, showing the strongly anterior position of eyes, paucity of abdominal segments, and scorpioid contraction of body. 1/1.

Slimonia, Page (*Himantopterus*, Salter), (Fig. 1422). Body attaining a length of 60 cm., and width of 15 cm. Cephalothorax sub-quadrate, with anterior marginal eyes and median ocelli. Preoral appendages in the form of small stout pincers, much like chelicerae in *Limulus*, but probably masticatory rather than prehensile. Of the five pairs of postoral appendages, the first is modified to form tactile organs, and is small and chelate; the second also slender and probably tactile. The first seven abdominal segments much wider than the rest, and divisible into two parts, a dorsal (*tergite*) and a ventral (*sternite*). The first two sternites are represented by the genital plate and its posterior divisions; the other five are discontinuous plates bearing branchial lamellae on their inner surface. The five posterior segments are long, narrow, and cylindrical. Telson like that of *Pterygotus*, but produced into a longer spine. Only one species. Old Red Sandstone; Scotland.

Stylonurus, Page. Body similar in general proportions to *Pterygotus*, and often exceeding 1 m. in length. Cephalothorax quadrate or sub-pentagonal, its margins

bent under so as to cover more than one-half of the ventral surface. Eyes large, approximate, sometimes surrounded by strong orbital ridges; ocelli on the slope of a median ridge. Preoral appendages known only by fragmentary chelicerae. Of the five pairs of postoral appendages, the first is chelate, the next two are short, and each joint bears a pair of lamellar processes. The last two pairs are enormously elongated, nine-jointed, extending almost to the end of the telson, and terminate in a sharp claw. Number of abdominal segments believed to be the same as in *Eurypterus;* each of the posterior segments sometimes bear a pair of detachable processes or epimera. Telson

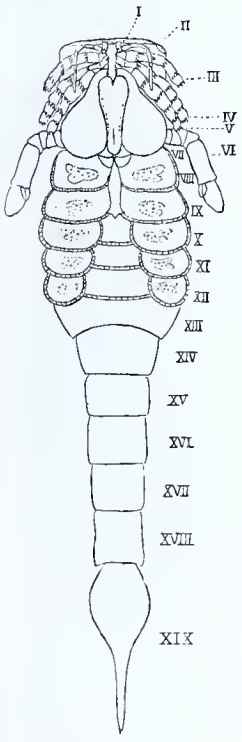


FIG. 1422.

Slimonia acuminata, Salter. Devonian; Lanarkshire, Scotland. Restoration of ventral surface, showing legs I.—VI. and abdominal segments VII.—XIX. The first five of the latter with branchial lamellae. 1/7 (after Laurie).

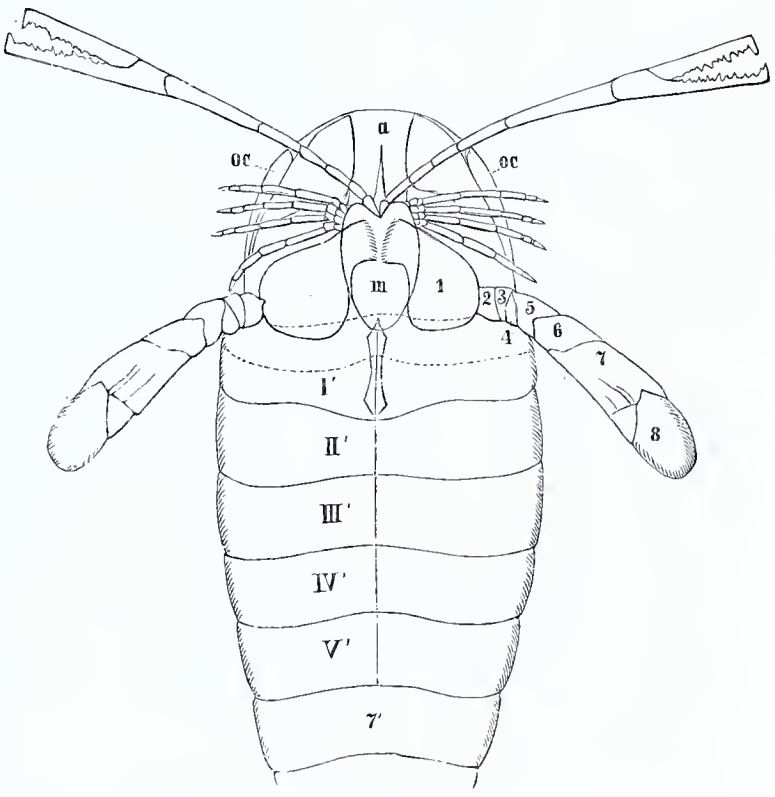


FIG. 1423.

Pterygotus Osiliensis, Schmidt. Silurian; Rootziküll, Island of Oesel. Restoration of ventral surface. *a*, Epistoma; *m*, Metastoma; *oc*, Eyes; I.—VI., Appendages, with joints numbered serially in the powerful swimming pair; I'.—V'., 7', First six abdominal segments. 1/3 (after F. Schmidt).

long and slender. Silurian and Devonian; Scotland. Upper Devonian; New York and Pennsylvania.

Pterygotus, Agassiz (Figs. 1423-1425). Gigantic Eurypterids, attaining a length of over 2 m. Cephalothorax semiovate, with anterior marginal eyes and central ocelli. Comb-like organs are present beneath the cephalothorax as in *Glyptoscorpius*. The metastoma is a heart-shaped plate attached along the middle line to the ventral wall of the cephalothorax, between the bases of the last pair of legs, and extending outwards and forwards so as to enclose the jaws in a kind of chamber. Epistoma a thin semicircular plate, occupying the same position as hypostoma in Trilobites, and having the preoral appendages attached close to its posterior border. The latter are large pincers, probably prehensile in function; by Schmidt and Woodward they are represented as many-jointed, but Laurie states them to consist of but three long joints. Behind the mouth are four pairs of slender walking legs, followed by the large

"swimming feet," which are similar to those in *Eurypterus*, except that they are less broadly expanded at the tips. Telson an oval plate, terminating in a slight projection. The species first referred to this genus (*P. problematicus*, Ag.) is but imperfectly understood, and *P. anglicus*, Ag., which is well known, is generally accepted as the typical form of the genus. Uppermost Silurian; Wales, Scotland, Oesel, New York. Old Red Sandstone; Scotland.

Erettopterus, Huxley and Salter. As in *Pterygotus*, but with a bilobed telson. Silurian; Lanarkshire.

Glyptoscorpius, Peach. Body attaining a length of 30 cm. Surface covered with highly developed scale-markings. Limbs ending in a double claw, as in scorpions, and the animal further provided with a pair of comb-like structures closely resembling the pectines of scorpions. Coal Measures; Scotland.

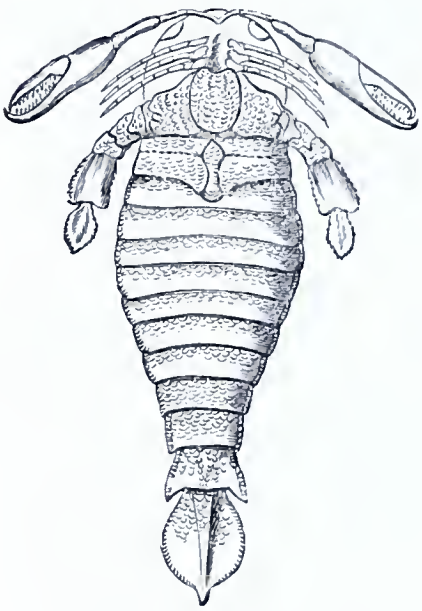


FIG. 1424.

Pterygotus anglicus, Agassiz. Old Red Sandstone; Forfarshire, Scotland. Restoration of ventral surface, but second pair of legs not represented. 1/5 (after Woodward).

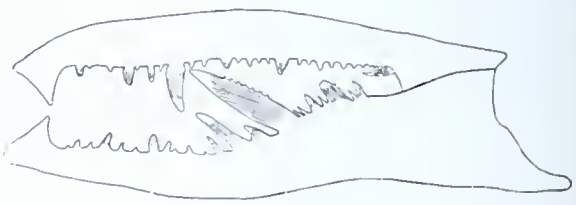


FIG. 1425.

Pterygotus Buffaloensis, Grote. Waterlime (Silurian); Buffalo, New York. The toothed antennal chela. 1/2.

[The chapter on the *Merostomata* was outlined in substantially its present form by Dr. John M. Clarke, of Albany, who furthermore contributed a number of new illustrations, both for this section and others on the *Eucrustacea* which he has revised for this work. Some additional details were introduced under the generic diagnoses by the Editor, and the whole text finally subjected to the criticism of Dr. J. S. Kingsley and the Author.—TRANS.]

Sub-Class 2. ARACHNIDA. Spiders, Scorpions, Mites, etc.

Acerata with six pairs of limbs around the mouth, at least four of which are ambulatory in function. Eyes simple, variable in number. Respiration by lung-books or by tracheae, these in either case developed from gill leaves arising on the posterior surface of one or more abdominal appendages. Cephalothorax usually without signs of segments dorsally. Abdomen sometimes clearly segmented, sometimes with the segments obsolete, and apodal. Malpighian tubes, when present, ectodermal in origin.

Six of the eight orders into which living Arachnids are divided occur in the fossil condition, and of these the scorpions, spiders, and *Pedipalpi* have existed ever since the Palaeozoic. By far the greatest number of species is preserved in amber of Lower Oligocene age from East Prussia. This fossil gum acts as a marvellous preservative, the most delicate parts, including the finest hairs and even spiders' webs, remaining practically unaltered.

The order *Acari* (Mites, Ticks) comprises forms in which the cephalothorax is anchylosed with the unsegmented abdomen. Fossil representatives occur in amber or fresh-water deposits of the Tertiary, and belong with few exceptions to recent genera.

The order *Chelonethi* (False Scorpions) is distinguished from the *Acari* by having a segmented abdomen. The recent genus *Chelifer* (Fig. 1426) occurs fossil in amber.

The order *Anthracomarti*, as defined by Karsch and Scudder, is restricted to the Carboniferous. The cephalothorax and abdomen are distinct, and the latter is composed of four to nine segments. The cephalothorax frequently presents wedge-shaped segments below. Examples: *Arthrolycosa*, Harger (Fig. 1427); *Poliochera*, *Geraphrynus*,

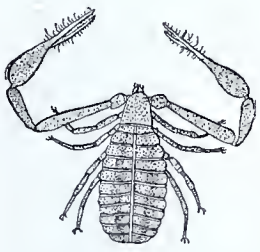


Fig. 1426.

Chelifer Hemprichii, Menge. Oligocene; Baltic amber. Copy, 9/1.

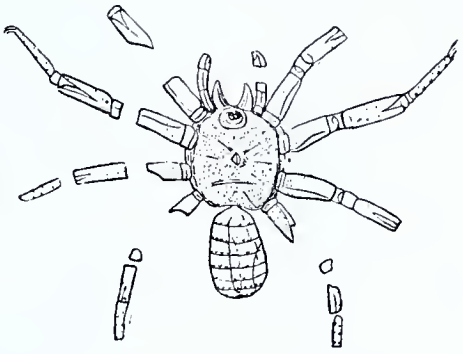


Fig. 1427.

Arthrolycosa antiqua, Harger. Coal Measures; Mazon Creek, Illinois. 1/1 (after Beecher).

Fig. 1428.

Architarbus rotundatus, Scudd. Coal Measures; Mazon Creek, Ill. Under surface, 1/1.

Architarbus, Scudder (Fig. 1428); *Anthracomartus*, Karsch (Fig. 1429); *Kreischeria*, Geinitz; *Eophrynus* (Fig. 1430), *Brachypyge*, Woodw.; *Phalangiotarbus*, Haase, etc.

The order *Pedipalpi* has the first pair of legs exceptionally long; cephalothorax and abdomen distinct; and some forms with a setigerous postabdomen. Certain

Fig. 1429.

Anthracomartus Voelkelianus, Karsch. Carbon Coal Measures; Neurode, Silesia. Dorsal surface, 1/1 (after Karsch).

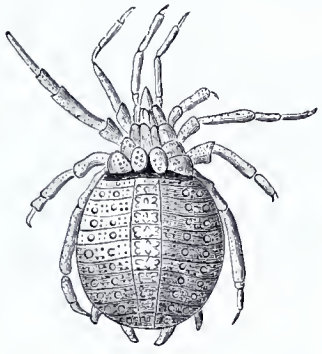


Fig. 1430.

Eophrynus Prestwichii, Buckland sp. Coal Measures; Coalbrookdale, England. Dorsal surface, 1/1 (after Woodward).

Fig. 1431.

Geralinura Bohemica, Kušta sp. Coal Measures; Rakonitz, Bohemia. 1/1 (after Kušta).

fragments from the Devonian of New Brunswick are referred here by Matthew. *Geralinura*, Scudder (Fig. 1431), is Carboniferous; *Stenarthron*, Haase, occurs in the Lithographic Slates of Bavaria. *Phrynus*, Latr., is Tertiary and Recent.

In the order *Scorpiones* the posterior end of the body consists of a preabdomen with seven segments, and a long slender postabdomen of six segments, the last of which forms a hollow poisonous sting. Scorpions are among the oldest of Arachnids. *Palaeophonus*, Thorell (Fig. 1432), and *Proscorpius*, Whitf., are known from the Silurian. *Eoscorpius*, M. and W. (Fig. 1433), *Centromachus*, Thorell, and *Cyclophthalamus*, Corda, are Carboniferous genera. A species of *Tityus*, Koch, is found in amber.

The order *Opiliones* is distinguished from true spiders by having the cephalothorax and abdomen fused. A number of species occur in amber, and according to Haase, most of the *Anthracomarti* should be placed here. The *Araneae* (Spiders) have numerous fossil representatives, at least one genus, *Protolycosa* (Fig. 1434), occurring as early as the Carboniferous. The majority, however, are found in

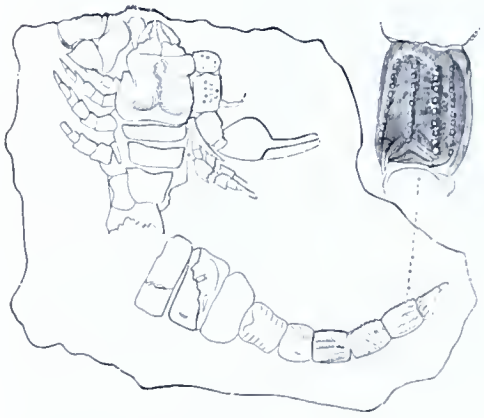


Fig. 1432.

Palaeophonus nuncius, Thorell and Lindström. Silurian; Wisby, Gottland. 1/1 (after Thorell).

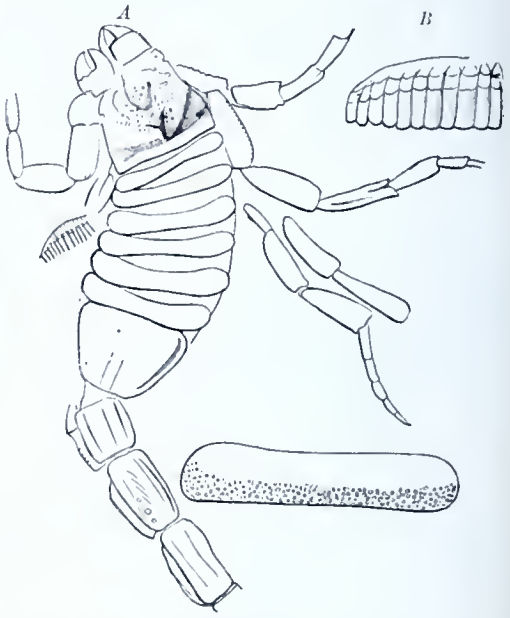


Fig. 1433.

Eoscorpius carbonarius, Meek and W. Coal Measures; Mazon Creek, Illinois. *A*, 1/1. *B*, Peeten, enlarged.

Oligocene amber (Fig. 1435); the lignites of Rott; fresh-water marls of Aix in

Fig. 1434.

Protolycosa anthracophila, Roemer. Coal Measures; Myslowitz, Silesia (after F. Roemer).

Fig. 1435.

Mizalia rostrata, Koch and Berendt. Oligocene; Baltic amber. Copy, 3/1.

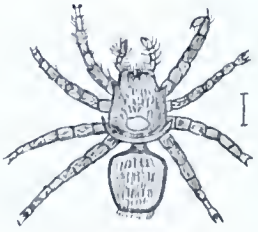


Fig. 1436.

Attoides ersiformis, Brongt. Oligocene; Aix, Provence. 10/1 (after Brongniart).

Fig. 1437.

Thomisus Oeningensis, Heer. Miocene; Oeningen, Baden. 2/1 (after Heer).

Provence (Fig. 1436); Oligocene fresh-water strata of Florissant, Colorado; and the Miocene of Oeningen, Baden (Fig. 1437).

TABLE SHOWING THE VERTICAL RANGE OF THE ARACHNIDA.[1]

Orders.	Silurian.	Devonian.	Carboniferous.	Permian.	Trias.	Jura.	Cretaceous.	Eocene.	Oligocene.	Neocene.	Recent.
Acari	.....	.....	.....	.....	.....	.....	.....	.....	34	2	*
Chelonethi	.....	.....	.....	.....	.....	.....	.....	.....	9	.....	*
Anthracomarti	.....	.....	16								
Pedipalpi	.....	.....	2	.....	.....	.....	.....	.....	.....	.....	*
Scorpiones	3	.....	8	.....	.....	.....	.....	.....	1	.....	*
Opiliones	.....	.....	.....	.....	.....	.....	.....	.....	13	.....	*
Araneae	.....	.....	2	.....	.....	.....	.....	.....	211	15	*

Sub-Phylum B. Myriopoda.

Tracheate Arthropods with distinctly separated head and numerous fairly similar segments, each of which bears one or two pairs of legs. Body vermicular, apterous. Head with one pair of antennae and three pairs of jaws.

The head in Myriopods is formed by a single division, which only in exceptional cases is supplemented by parts of the following body segments. The two most important orders are *Chilopoda* and *Diplopoda*. In the former, which approaches very closely to Insects, every body segment possesses a single dorsal and a ventral plate, to which a pair of legs is attached. The Diplopods, on the other hand, show on every segment except the first a dorsal plate and two ventral plates, with two pairs of legs.

Fig. 1438.

Archidesmus Macnicoli, Peach. Devonian; Forfarshire, Scotland. 1/1 (after Peach).

A precursor of the Chilopods is found in the genus *Palaeocampa*, M. and W., from the Carboniferous, whose body is composed of but a few segments. Scudder places it in a distinct order, *Protosyngnatha*. True Chilopod genera (*Cermatia*, Rossi; *Scolopendra*, Linn.; *Lithobius*, *Geophilus*, Leach) occur in amber and the fresh-water gypsum of Aix, Provence.

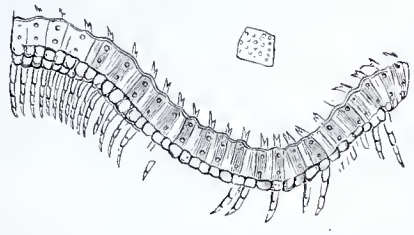


Fig. 1439.

Euphoberia armigera, Meek and W. Coal Measures; Mazon Creek, Illinois. 1/1.

Most Palaeozoic Myriopods are of large size and belong to the order *Archipolypoda*, in which all body segments possess two dorsal and two ventral plates, with two pairs of legs. Two genera are found in the Old Red Sandstone of Scotland, *Archidesmus*, Peach (Fig. 1438); and *Kampecaris*, Page. Numerous others occur in the Carboniferous and Trias of both continents, and some have been recognised by Matthew in the Devonian of New Brunswick. Examples: *Euphoberia*, M. and W. (Fig. 1439); *Amynilispes*, Scudder; *Xylobius*, Dawson; *Acantherpestes*, M. and W., a genus regarded by Scudder as probably amphibious.

From Mesozoic rocks but a single species is known (*Julopsis cretacea*, Heer).

[1] The figures indicate the number of species, as estimated in 1885.

Several Diplopods are found in the Tertiary, especially in amber. Examples: *Julus*, Linn. (Fig. 1440); *Craspedosoma*, Leach; *Euzonus*, Menge; *Polyxenus*, Latr.; *Phryssonotus*, Scudder (*Lophonotus*, Menge).

Fig. 1440.

Julus antiquus, Heyden. Miocene; Rott, near Bonn, Germany. Copy, 1/1.

Sub-Phylum C. Insecta (*Hexapoda*). Insects.[1]

Tracheate Arthropods with body at maturity consisting of three divisions—head, thorax, and abdomen; supplied with a pair of antennae on the head, three pairs of legs, and usually two pairs of wings on the thorax. The latter is composed of three, and the abdomen of nine or ten segments. Development usually through metamorphic stages.

Fossil Insects can be referred, usually without difficulty, to the existing orders of *Aptera*, *Orthoptera*, *Neuroptera*, *Hemiptera*, *Coleoptera*, *Diptera*, *Lepidoptera*, and *Hymenoptera*. The Palaeozoic forms, however, show a less marked differentiation in the structure of their wings and are more closely related to each other than their successors of the corresponding orders. Scudder, on this account, unites these primitive precursors by placing them in a special group (*Palaeodictyoptera*), and compares its representatives, under the names of *Orthopteroidea*, *Neuropteroidea*, *Hemipteroidea*, and *Coleopteroidea*, with the typical *Orthoptera*, *Neuroptera*, etc., of later date.

The researches of C. Brongniart[2] regarding the rich Palaeozoic fauna of Commentry, although they lead to the conclusion that strangely differentiated forms occurred in the different groups even in the Carboniferous, show even more conclusively than before that this differentiation had little depth, and that it is only through their presumable descendants that we have any claim to a wide separation of the original Palaeozoic forms. The neuration of the wings, though diversified, had yet a far greater homogeneity than is found now, or than existed during Mesozoic time. The fore wings of whatever type were as diaphanous as the hind, and could never (as in most of their descendants) properly be called *tegmina*. The wings of the *Protodonata* (Fig. 1260) of Brongniart had indeed a superficial resemblance to living *Odonata* in shape, reticulation, and sweep of the veins; but in fundamental neuration they were altogether different, and they wholly lacked any sign of those characteristic features of the *Odonata*, termed the *nodus*, *triangle*, and *pterostigma*, which appear fully developed in the Mesozoic species. Nor should it be forgotten how highly probable it is that the Lepidopteran, Dipteran, and Hymenopteran phyla had their origin in types already recognised in the Palaeozoic. In a text-book, however, and perhaps in any general treatise, it may be best to bring the *Orthopteroidea*, *Neuropteroidea*, etc., in direct connection with the *Orthoptera*, *Neuroptera*, etc., as indicative of the precise phylogeny of the latter groups.

Order 1. APTERA.

Wingless insects with hairy or scaly body covering; with rudimentary masticating mouth parts and setiform anal filaments, which may serve as a springing apparatus, at the end of the ten-segmented abdomen. Development without metamorphosis.

[1] [The most complete guides to the literature of fossil Arachnids, Myriopods, and Insects are to be found in the writings of Professor Samuel H. Scudder, of Cambridge, Mass., who has revised the translation of these chapters for the present work—without, however, having altered their systematic arrangement. One should consult especially his collection of papers in two volumes, entitled *Fossil Insects of North America* (New York, 1890); *Bulletin of the United States Geological Survey*, Nos. 31, 69, 71, 93, 101, 124; Vol. XIII. of the *Annual Reports;* and XXI. of the Survey *Monographs* (Washington, 1886-95); also his discussion of the above-named groups in *Zittel's Handbuch der Palaeontologie*, Vol. II. (Munich and Leipsic, 1885).—Trans.]

[2] See his important work: *Recherches pour servir a l'histoire des insectes fossiles des temps primaires*, 2 vols., St. Etienne, 1893.

To this lowly organised class of insects belong the *Thysanura* and *Collembola* (Spring-tails). Brongniart describes a species of the first group from the Carboniferous of Commentry (*Dasypeltus Lucasi*), which resembles the living *Lepisma*, but has only a single terminal filament. In amber and the Oligocene of Florissant a number of species are found, some of which belong to still living, and others to extinct genera. Examples: *Petrobius* (Fig. 1441), *Lepidion*, *Forbicina*, *Machilis*, etc. *Planocephalus*, a headless form from the Oligocene of Colorado, is regarded by Scudder as the type of a distinct sub-order.

Fig. 1441.

Petrobius seticornis, Koch and Berendt. Oligocene; Baltic amber. Copy, $^2/_1$.

Order 2. ORTHOPTERA.

Fore wings coriaceous, hind wings thinner, delicately veined, plicated. The five principal veins of the wings, with all their branches, extend to the outer margin of the wing. Jaws adapted for biting. Metamorphosis incomplete.

Palaeozoic representatives of this order frequently combine characters which are at present distributed among different families. The neuration of their wings also shows

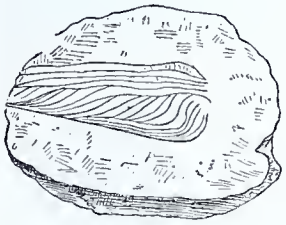


Fig. 1442.

Palaeoblattina Douvillei, Brongt. Silurian; Jurques, Calvados. $^2/_3$ (after Brongniart).

Fig. 1443.

Aedocophasma Anglica, Scudder. Coal Measures; England. $^1/_1$.

a less marked differentiation than is the case in more recent *Orthoptera;* moreover, the fore and hind wings differ less decidedly from each other than in the later forms.

An isolated wing from the Middle Silurian of Jurques, Calvados (*Palaeoblattina Douvillei*, Brngt., Fig. 1442), is one of the oldest of fossil insect remains, but does not admit of closer determination; Brongniart no longer regards it as a cockroach. The Carboniferous of North America and Europe yields numerous genera and species, which are more or less closely related to typical *Orthoptera.* Some of these are of gigantic proportions. The richest localities for remains of this order are Commentry, France; Saarbrücken and Halle, Germany; Illinois; Ohio; and West Virginia. Many genera are known only by detached wings. Among the largest and best preserved forms are *Protophasma*, *Stenoneura*, *Aedoeophasma* (Fig. 1443), and *Paolia.* Smaller forms include *Polioptenus* (Fig. 1444); *Oedischia* with saltatorial hind legs; *Stethaneura*, *Caloneura*, and *Ischnoneura.* Cockroaches, however, were the prevailing type during the Palaeozoic, fully 200 species being known, belonging to the genera *Etoblattina*, *Gerablattina*, *Anthracoblattina*, *Progonoblattina* (Fig. 1445), *Mylacris*, etc. *Spiloblattina* from the Trias is placed in the same group as the Palaeozoic forms, under the name of *Palaeo-*

Fig. 1444.

Polioptenus elegans, Goldenbg. sp. Coal Measures; Saarbrücken, Germany. $^1/_1$.

blattariae, Scudder. According to Brongniart, the female was, in some cases at least, provided with a long ovipositor.

Fig. 1445.

Progonoblattina Columbiana, Scudder. Coal Measures; Mazon Creek, Illinois. 2/1.

The *Forficulidae* (Earwigs) are found in the Lias of Aargau, in amber, and in the Tertiary of Aix, Oeningen, Monte Bolca, and Florissant.

True *Blattariae* (Cockroaches proper) begin in the Trias of Colorado and Europe, and occur quite abundantly in the Lias of Schambelen, Aargau, and in the Upper Jura of England and Bavaria. They have also been shown to exist in amber and in different Tertiary localities. Examples: *Scutinoblattina*, *Neorthroblattina*, *Legnophora*, Trias. *Blattidium*, *Rithma*, *Mesoblattina*, *Blabera*, Jura.

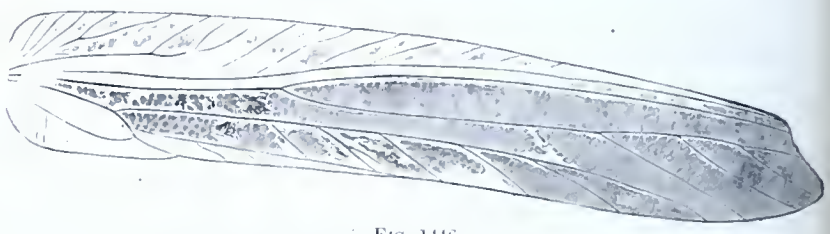


Fig. 1446.

Drymadusa speciosa, Heer sp. Miocene; Oeningen, Baden. 2/1.

Fossil remains of *Mantidae* and *Phasmidae* (Walking Sticks) occur rarely in the Tertiary. The *Aeridiidae* (Grasshoppers); *Locustidae* (Locusts, Fig. 1446); and *Gryllidae* (Crickets, Fig. 1447) are known from the Lias onward, and are not uncommon in the Tertiary. A large grasshopper, *Locusta speciosa*, Münst., is found in the Lithographic Slates of Bavaria. *Pygolampis gigantea* (*Chresmoda obscura*) is considered by Haase as also a precursor of *Mantidae* and *Phasmidae*.

Fig. 1447.

Gryllus macrocercus, Germar. Oligocene; Baltic amber. 3/2 (after Germar).

Order 3. NEUROPTERA.

Both pairs of wings large, of nearly equal size, membranous, and traversed by numerous delicate reticulated nervures. Antennae simple. Metamorphosis complete or incomplete.

Fig. 1448.

Proptetieus infernus, Scudder. Coal Measures; Illinois. 3/2 (after Scudder).

Like the *Orthoptera*, Palaeozoic forms of this order are characterised by their meagre differentiation, and are called by Scudder *Neuropteroidea*. Unless *Palaeoblattina* (see above) belongs here, the oldest fossil remains are found in the Devonian of New Brunswick (*Lithentomum*, *Xenoneura*, *Homothetus*). A very considerable number of genera, in part well preserved, are known from the Carboniferous of Commentry, Saarbrücken, Bohemia, Saxony, Great Britain, and Illinois. Examples: *Acridites*, *Palingenia*, *Genentomum*, *Proptetieus* (Fig. 1448), *Strephocladus*, *Lithomantis* (Fig. 1449), *Lithosialis*, *Brodia*, *Chrestotes*, *Hemeristia*, *Megathentomum*, *Miselioptera*, *Psilothorax*, *Sphecoptera*, *Corydaloides*, *Homaloneura*, *Blanchardia*, *Compsoneura*, *Meganeura* (Fig. 1260, p. 604), etc.

The family *Termitidae* (White Ants) begins in the Lias, and is well represented in the Tertiary, especially in amber, the Oligocene of Florissant, and Miocene of Rott,

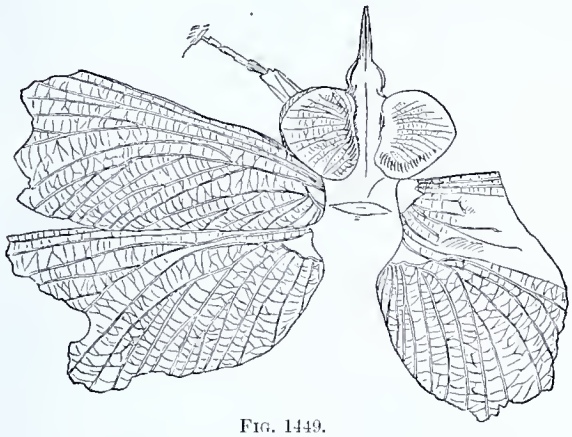


Fig. 1449.

Lithomantis carbonaria, Woodward. Coal Measures; Scotland. 2/3 (after Woodward).

Fig. 1450.

Cronicus anomalus, Pictet sp. Oligocene; Baltic amber. 3/2 (after Pictet).

Oeningen, and Rodoboj. One unusually large species, *Gigantotermes* (*Apochrysa*) *excelsa*, Haase, appears as early as the Lithographic Slates of Bavaria.

Psocidae (Book-lice), *Embidae*, and *Perlidae* sometimes occur in amber. *Ephemeridae* (May Flies), whose precursors are found in Palaeozoic rocks, are

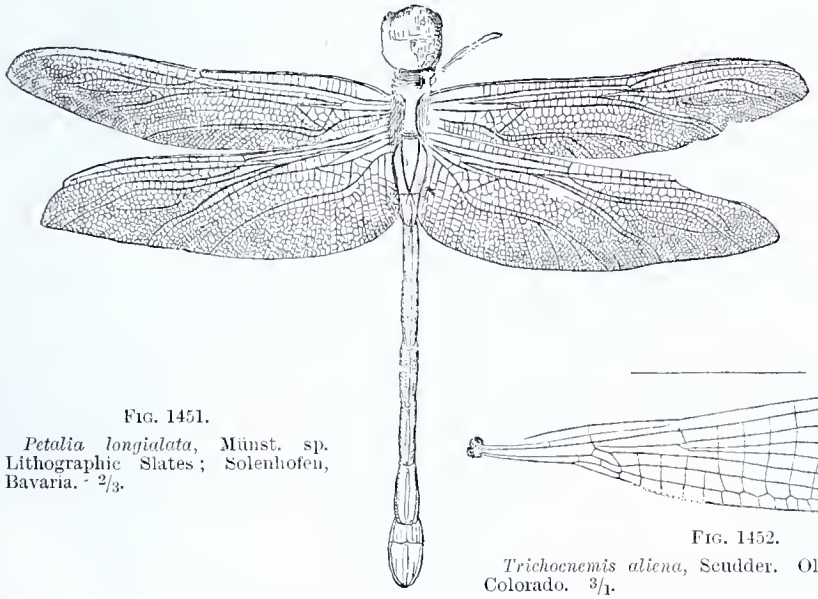


Fig. 1451.

Petalia longialata, Münst. sp. Lithographic Slates; Solenhofen, Bavaria. 2/3.

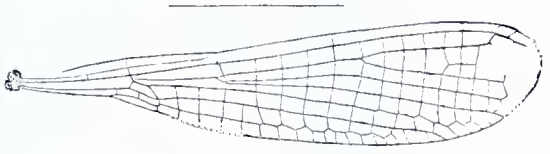


Fig. 1452.

Trichocnemis aliena, Scudder. Oligocene; Florissant, Colorado. 3/1.

preserved in the Lithographic Slates, in amber (Fig. 1450), and in certain Tertiary deposits.

Especial interest centres in the numerous and excellently preserved remains of *Odonata* (Dragon Flies) from the Lithographic Slates of Bavaria, such as *Petalia* (Fig. 1451), *Stenophlebia*, *Isophlebia*, *Aeschna*, *Anax*, *Heterophlebia*, etc. The group begins in the Lias, but is hardly so well represented in the Tertiary as would be expected. *Trichocnemis* (Fig. 1452). Oligocene.

Fossil remains of *Sialidae*, *Hemerobidae* (Lace-winged Flies), *Panorpidae*, and *Phryganidae* (Caddis Flies) are first met with in the Trias and Jura, and increase considerably in numbers during the Tertiary. Ootheca of gigantic *Sialidae* (*Corydalites*) are known from the Laramie Beds of Colorado, and from the Garumnien (Uppermost Cretaceous) of Provence. The tubular larval cases of *Phryganidae* from the Tertiary are sometimes 2-3 m. thick (*Indusienkalk*, *calcaire à induses*, of Anvergne).

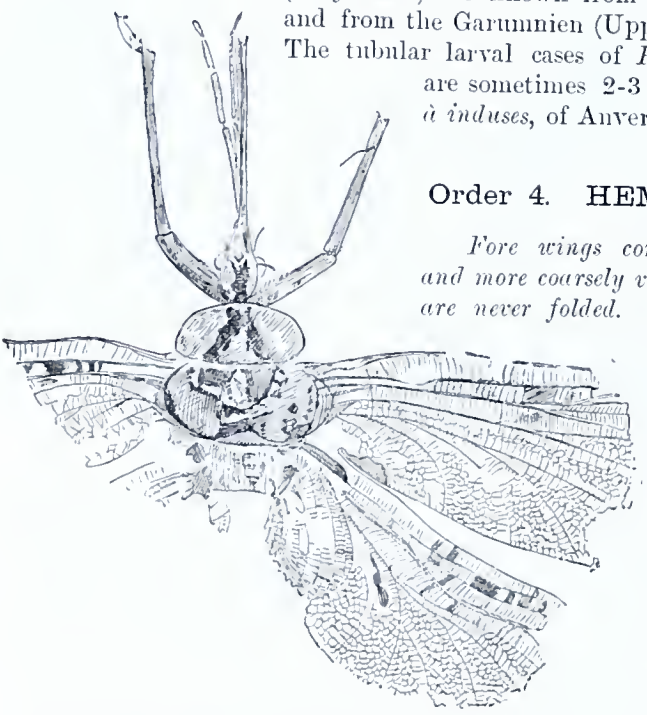


Fig. 1453.

Eugereon Boeckingi, Dohrn. Permian; Birkenfeld, Oldenburg. 3/4 (after Dohrn).

Order 4. HEMIPTERA. (Rhynchota.)

Fore wings coriaceous or membranous, larger and more coarsely veined than the hind wings, which are never folded. Mouth with jointed, beak-like, suctorial rostrum. Metamorphosis incomplete.

The oldest known fossil insect is a somewhat obscure wing, plainly Hemipterous (*Protocimex silurica*, Moberg), from the Graptolite Slates of the Swedish Upper Ordovician. Carboniferous genera are *Fulgorina*, *Dictyocicada*, *Mecynostoma*, and *Phthanocoris*. The first-named is also found in the Permian, together with the remarkable genus *Eugereon* (Fig. 1453), which has large, membranous, reticulated fore and hind wings, prolonged lancet-like mouth parts, and filiform antennae.

The oldest remains of *Aphidae* (Plant-lice) are found in the Wealden, and numerous species occur in the Tertiary. *Coccidae* (Scale Insects), *Fulgoridae*, *Membracidae*, *Cicadellidae*, and *Cicadidae* (Harvest Flies) are tolerably abundant in the Tertiary, especially in amber. Most of the families

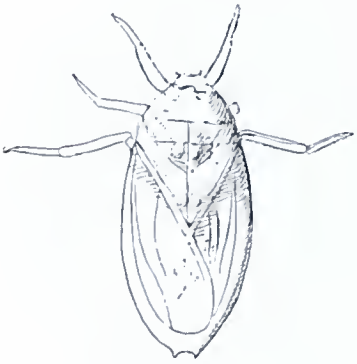


Fig. 1454.

Scarabaeides deperditus, Germar. Lithographic Slates; Eichstadt, Bavaria. 2/3.

Fig. 1455.

Naucoris dilatatus, Heer. Miocene; Oeningen, Baden. 1/1 (after Heer).

Fig. 1456.

Harpactor maculipes, Heer. Miocene; Oeningen, Baden. 1/1 (after Heer).

are represented as early as the Lias, or even by scanty remains in the Trias (*Cercopyllis*, from Colorado). *Cercopidium* occurs in the Lias of Dobbertin. *Eocicada* and *Prolystra* in the Lithographic Slates of Bavaria.

Of the aquatie bugs, a number of families are met with in the Jura, such as the *Nepidae*, *Hydrometridae*, *Reduviidae*, *Lygaeidae*, *Coreidae*, *Thripsidae*, and *Cimicidae*. *Scarabaeides* (Fig. 1454) occurs in the Bavarian Lithographic Slates. Examples of Tertiary genera are: *Naucoris* (Fig. 1455), *Harpactor* (Fig. 1456), *Cephalocoris* (Fig. 1457), *Berytopsis*, *Acanthosoma*, and *Eothes*.

Fig. 1457.

Cephalocoris pilosus, Heer. Miocene; Oeningen, Baden. $^3/_1$ (restored after Heer).

Order 5. COLEOPTERA. Beetles.

Fore wings (elytra) chitinous, thick, with obsolete nervures; hind wings membranous, folded, with nervures connected only at wide intervals. Prothorax freely movable. Mouth parts masticatory. Metamorphosis complete.

Coleopterous remains have not been recognised with certainty in the Palaeozoic. *Dipeltis* is of doubtful position, but bears a certain resemblance to the larvae of beetles. During the Mesozoic and Tertiary, however, this group occupies a prominent position among insects.

Remains of *Curculionidae*, *Chrysomelidae*, and *Buprestidae* are found in the Trias of Vaduz and Rutihärd, near Basle; and the same families occur more abundantly in the Rhaetic and chief divisions of the Jura in Europe. Among the richest Mesozoic localities may be mentioned: Schambelen in Aargau (Lias); Dobbertin, Mecklenburg (Lias); Stonesfield Slate and Purbeck of England (Figs. 1458, 1459). The Bavarian Lithographic Slates yield comparatively few, and for the most part poorly preserved remains of beetles (*Pseudohydrophilus*, *Chrysobothris*).

Fig. 1458.

Cyphon vetustus, Giebel. Purbeck; Vale of Wardour, England. $^6/_1$ (after Brodie).

Fig. 1459.

Cerylon striatum, Brodie. Purbeck; Vale of Wardour, England. $^1/_1$ (after Brodie).

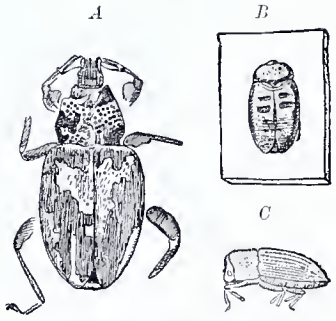


Fig. 1460.

Fossil Beetles from the Oligocene marls of Aix, Provence. *A*, *Hipporhinus Heeri*, Oustalet. $^2/_1$. *B*, *Triphyllus Heeri*, Oustalet. $^5/_1$. *C*, *Hylesinus facilis*, Heer. $^4/_1$.

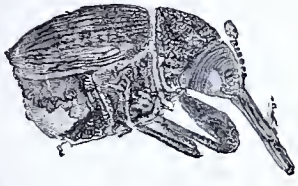


Fig. 1461.

Paltorhynchus rectirostris, Scudder. Oligocene; Florissant, Colorado. $^5/_1$.

Fig. 1462.

Apion refrenatum, Scudder. Oligocene; Florissant, Colorado. $^{12}/_1$.

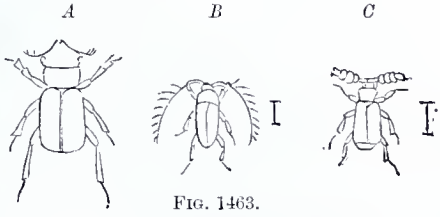
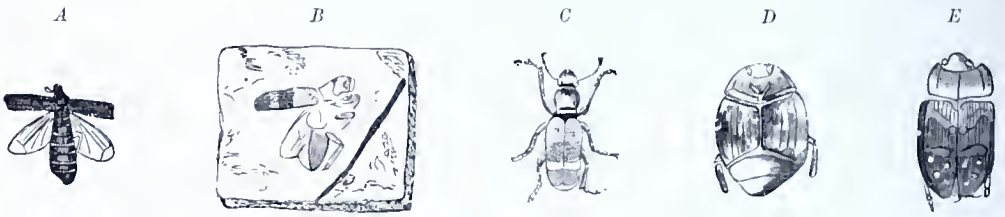


Fig. 1463.

Beetles from Oligocene amber of East Prussia. *A*, *Dorcasoides bilobus*, Motsch. $^3/_1$. *B*, *Ptilodactyloides stipulicornis*, Motsch. $^3/_1$. *C*, *Paussoides Mengei*, Motsch. $^2/_1$.

A marked increase took place during the Tertiary, and by far the greater number of species are referred to still living genera. The Oligocene fresh-water deposits of Aix in Provence (Fig. 1460), and of Florissant, Colorado (Figs. 1461, 1462), are especially rich in species; also the amber of East Prussia (Fig. 1463), Miocene

lignites of Rott, Sieblos, Westerwald, Kutschlin in Bohemia, the fresh-water marls of Oeningen, Baden (Fig. 1464), and certain localities in Croatia, Italy, Utah, and



[Fig. 1464.

Beetles from the Miocene fresh-water marls of Oeningen, Baden. *A*, *Lytta Aesculapii*, Heer. $^1/_2$. *B*, *Clerus Adonis*, Heer. $^1/_1$. *C*, Same restored. *D*, *Hister marmoratus*, Heer. $^2/_1$. *E*, *Nitidula maculigera*, Heer. $^2/_1$.

Wyoming. Of the rhynchophorous families alone about 350 Tertiary species have been described, most of which are excellently preserved. Perhaps the most curious form is *Triaena*, a parasitic Stylopid from amber.

Order 6. DIPTERA. Flies.

Fore wings membranous, narrow, veined. Hind wings reduced to clubbed filaments (halteres). Mouth parts adapted for piercing and sucking. Metamorphosis complete.

Fossil flies are first encountered in the Lias (*Maeropeza*), but most of the Jurassic forms are too poorly preserved for accurate identification. *Musca*, *Cheilosia*, and *Empidia* are known from the Lithographic Slates; *Corethrium*, *Ceecidomium*, and *Rhyphus* from the English Purbeck.

The Tertiary, especially Oligocene and Miocene, yields large numbers of flies, *Tipulidae* (Crane Flies) and *Bibionidae* being the most abundant. Other families represented are: *Syrphidae*, *Muscidae*, *Oestridae* (Bot Flies), *Agromyzidae*, *Platypezidae*,

Fig. 1465.

Psilites bella, Heer. Miocene; Radoboj, Croatia. $^1/_1$ (after Heer).

Fig. 1466.

Empis Melia, Heyden. Miocene; Root, near Bonn, Germany. $^2/_1$ (after Heyden).

Fig. 1467.

Palembolus florigerus, Scudder. Oligocene; Florissant, Colorado. $^2/_1$ (after Scudder).

Fig. 1468.

Chironomus Meyeri, Heer. Miocene; Oeningen, Baden. $^6/_1$ (after Heer).

Psilidae (Fig. 1465), *Empidae* (Fig. 1466), *Bombylidae*, *Nemestrinidae* (Fig. 1467), *Asilidae* (Robber Flies), *Stratiomyidae*, *Chironomidae* (Fig. 1468), *Culicidae* (Gnats) *Mycetophilidae* (Fig. 1476), *Ceecidomyidae*, etc.

Order 7. LEPIDOPTERA. Butterflies and Moths.

Fore and hind wings similar, scaled, usually brilliantly coloured. Mouth parts suctorial, forming a spiral proboscis. Metamorphosis complete.

Lepidoptera are very rare in the fossil state, and known as yet only from the Tertiary. *Pseudosirex* (*Sphinx*) *Schroeteri*, from the Lithographic Slates of Bavaria, was considered a Lepidopteron by Oppenheim, but by Deichmüller as a wood-wasp (*Uroceridae*).

Most of the larger groups have isolated representatives in the Tertiary. The smaller moths (*Microlepidoptera*) occur in amber in various stages of development. Two species of *Phalaenidae* are known from Radoboj; a third is found at Aix, and another (*Lithopsyche*) in the Isle of Wight. Species of *Noctuidae* and several

FIG. 1469.

Prodryas Persephone, Scudder. Oligocene; Florissant, Colorado. 1/1.

FIG. 1470.

Barbarothea Florissanti, Scudder. Oligocene; Florissant, Colorado. 1/1. (after Scudder).

Bombycidae have been described from Aix and from Oeningen. Of the Hawk-moths (*Sphingidae*) *Sphinx* is found in amber, and *Sesia* at Aix. Butterflies are very rare, but about a dozen genera are known from the fresh-water strata of Aix. Rott, Radoboj, and Florissant. From the last-named locality *Prodryas* (Fig. 1469) is exquisitely preserved. Two of the eight species known from this rich locality (*Prolibythea*, *Barbarothea*, Fig. 1470) belong to the now nearly extinct but widespread group of *Libytheinae*.

Order 8. HYMENOPTERA.

Fore wings larger than the hind pair, thin, membranous, with few and separated nervures. Mouth parts adapted for biting and licking. Prothorax fused. Metamorphosis complete.

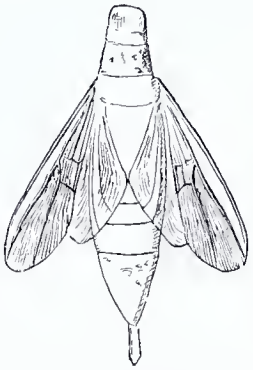


FIG. 1471.

Belostomum elongatum, Germar. Lithographic Slates; Eichstadt, Bavaria. 2/3.

FIG. 1472.

Atocus defessus, Scudder. Oligocene; Florissant, Colorado. 3/1.

The oldest *Hymenoptera* occur in the Lias of Schambelen in Aargau, and belong to the ants. *Apiaria*, *Belostomum* (Fig. 1471), and *Pseudosirex* have been described from the Lithographic Slates; *Formicium* and *Myrmicium* from the Purbeck. All other remains are of Tertiary age, and belong to the *Tenthredinidae* (Fig. 1472),

Uroceridae (Wood Wasps), *Cynipidae* (Gall Flies), *Ichneumonidae* (Fig. 1473), *Braconidae*, *Chrysididae* (Gold Wasps), *Vespidae* (Wasps), *Apidae* (Bees, Fig. 1474), *Formicidae* (Ants, Fig. 1475), etc. They are most abundant in amber, and in the

Fig. 1473.

Ichneumonites bellus, Heer. Miocene; Oeningen, Baden. $^5/_2$ (after Heer).

Fig. 1474.

Xylocopa senilis, Heer. Miocene; Oeningen, Baden. $^1/_1$ (after Heer).

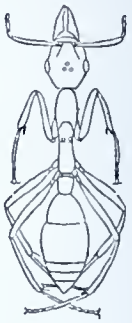


Fig. 1475.

Prionomyrmex longiceps, Mayr. Oligocene; Baltic amber. $^2/_1$ (after Mayr).

fresh-water strata of Aix, Oeningen, and especially Radoboj and Florissant. A species of *Myrmar*, one of the minutest insects known, belonging to the parasitic *Proctotrupidae*, has been found in Baltic amber.

Range and Distribution of the Insecta.

According to Scudder, about 2600 fossil insects had been described up to 1885, of which 155 were Palaeozoic species, 475 Mesozoic, and 1972 Tertiary. Since then these figures have been considerably increased by discoveries at Commentry, Florissant, in amber and elsewhere.

The oldest fossil insect is *Protocimex* from the Swedish Ordovician. Following this are *Palaeoblattina* from the Middle Silurian of Calvados, France, and several Devonian forms from New Brunswick.

A marked increase in numbers and variety of form is observed in the Coal Measures, the most noted localities being Commentry in Department Allier, and Mazon Creek, Illinois. Other localities for the older fossil insects are Zweibrücken, Wettin-Löbejün near Halle, Manebach in Thuringia, the Belgian and British coal-fields in Europe, and Nova Scotia, Pennsylvania, Ohio, and Rhode Island in America.

The Permian (especially the Rothliegendes of Weissig in Saxony, Stockheim in Bavaria, Lebach near Saarbrücken, and Cassville, West Virginia) yields few, but in part very interesting species, for example, those of *Eugereon*. From different localities of the Trias, Heer describes several *Orthoptera*, and also two beetles from Vaduz in Liechtenstein. To these must be added about twenty species recently discovered in the South Park of Colorado, nearly all of which are cockroaches. The Lias of Schambelen in Aargau, Dobbertin in Mecklenburg, and Gloucestershire, England, contains a tolerably rich insect fauna. Only a few species are derived from the Stonesfield Slates, but the Purbeck of Southern England, on the other hand, is quite rich. Excellently preserved remains are found in Lithographic Slates (Upper Jura) of Bavaria, especially at Solenhofen, Eichstätt, and Kelheim. The Cretaceous again is very poor in insect remains, most of the forms occurring in Bohemia.

Some Eocene species are known, but for the most part not yet fully described, from the Isle of Wight and phosphorites of Quercy, France. The Oligocene insect fauna is surprisingly rich and varied. By far the greatest number of species is derived from Baltic amber; other interesting localities are Aix in Provence, Florissant, and the White River region of Colorado. The Miocene localities of

Oeningen in Baden, Radoboj, Parschlug, Rott on the Rhine, etc., are scarcely less rich than the Oligocene.

In the Pleistocene, the interglacial clays of Switzerland and of Ontario, Canada, the peats of Northern France and England, and the lignites of Hösbach, Bavaria, deserve mention as localities for fossil insects.

TABLE SHOWING THE VERTICAL RANGE OF FOSSIL INSECTS.

Orders.	Silurian.	Devonian.	Carboniferous.	Permian.	Trias.	Jura.	Cretaceous.	Tertiary.	Recent.
Aptera									
Orthoptera									
Neuroptera	?								
Hemiptera									
Coleoptera									
Diptera									
Lepidoptera									
Hymenoptera									

Fig. 1476.

Necromyza pedata, Scudder. Miocene; Oeningen, Baden. $^{12}/_{1}$ (after Scudder). See under *Diptera*, p. 688.

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[Names of genera and sub-genera regarded as synonyms are printed in *italics*, all others in Roman.]

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